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# RELATION OF TEMPERATURE TO THE ASCORBIC ACID CONTENT OF COWPEA PLANTS

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(WITH FIVE FIGURES)

Few investigations on the relation of temperature to the synthesis and accumulation of ascorbic acid have been reported and brief mention only (Reid 1941) has been made of its influence on metabolic losses of the vitamin in intact plants. Most of these reports have dealt with the effect of temperature on the percentage content of the vitamin at some particular stage of development. There is no previous work showing its effect on the total quantity of ascorbic acid at different stages of development.

Kuthy (1938) as a result of experiments with wheat, barley, oats, and corn stated that more ascorbic acid is formed at 15° than at 10° C. Povolockaja (1937a) found that a lowering of temperature retards germination and growth and tends to increase the vitamin C concentration. This was noted particularly in legumes. He found (1937a) that the rate of accumulation of vitamin C varies with the rate of respiration and concluded that the relation is not fortuitous but a causal one. Moldtmann (1939) germinated seeds of several different types in darkness at different temperatures and determined the ascorbic acid content when they had attained approximately the same size. The highest ascorbic acid values expressed as milligrams per cent was found in *Pisum sativum* and *Avena sativa* grown at relatively low temperatures (3° C.) and decreasing values toward a high temperature (30° C.). In *Zea mays* there was a slightly higher content at the higher temperatures than at 10° C. and in *Polygonum fagopyrum* definitely higher at 25° than in the lower temperatures employed (5° to 15°). There was no difference in the ascorbic acid content of *Vicia faba* at 5, 10, and 25° and in *Phaseolus vulgaris* a higher content at 10 and 15° than at 5 and 25° was found. Moldtmann concluded from his results that there is no agreement between germination temperature and the ascorbic acid content, —that the temperature which is most favorable for ascorbic acid synthesis varies in the different types. In tests with *Vicia faba* and *Pisum sativum* he reported that differences in temperature caused no change or only a slight



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change in ascorbic acid content but that relatively high temperatures definitely favored respiratory intensity.

Wolf (1938) studied the variations in the percentage content of ascorbic acid in detached leaves of *Bryophyllum calycinum* when kept in darkness at different temperatures. At 20° C. the ascorbic acid content quickly decreased, whereas at 7 and 37° it had decreased little after 48 hours in darkness.

## PROCEDURE

To determine the relation of temperature to ascorbic acid accumulation and growth, studies were conducted with young plants grown at different temperatures,[1] some in darkness and others in light. Seeds of uniform size were planted in washed white sand contained in glazed crocks of the shallow type. The cultures, containing twenty-five plants each, were kept uniformly moist with tap water. Tests were conducted with three groups of plants grown in darkness, one at 22°, another at 26°, and a third at 29° C. A humidity of approximately 80 per cent was maintained at each of the three temperatures. Four cultures, grown at each temperature were used in making daily determinations of the green weights, dry weights, and ascorbic acid content. With the indophenol method duplicate ascorbic acid assays were made, ten plants being used in each. Forty plants were used in each of the dry weight determinations. Similar tests were conducted with plants grown in daylight in the greenhouse, some at 24°, others at 29° C. Tests were conducted with and without the addition of nutrient solutions.

## OBSERVATIONS

*Experiments with Seedlings Grown in Darkness.* The maximum ascorbic acid values were lower but were reached earlier in the plants grown at 29° than in those grown at 26 or 22°. In one of the tests there was very little difference between the maximum at the two latter temperatures but in both tests those at 26° were reached earlier than those at 22°. There was little difference in the rate of increase at the two higher temperatures during the first four days, whereas at the lower temperature the rate was definitely lower. The maximum green weight was not attained until two days later than the maximum ascorbic values in each of the three groups of plants. The maximum green weight differences may be significant but the variations in different tests were not always in this order and were probably caused by slight differences in the original weights of the seeds used in different cultures. The total fresh weight and ascorbic acid values per plant at successive stages of growth in darkness under each of the three temperatures are shown in figure 1. The ascorbic acid curves have three phases: one, a period

[1] Temperature chambers in the Cold Storage Laboratory of the Division of Fruit and Vegetable Crops and Diseases, U.S.D.A., were employed in these experiments.

of very rapid accumulation at the two higher temperatures and somewhat less so at the lower, another of less rapid increase when the reserves in the cotyledons are nearing exhaustion, followed by a period of loss.

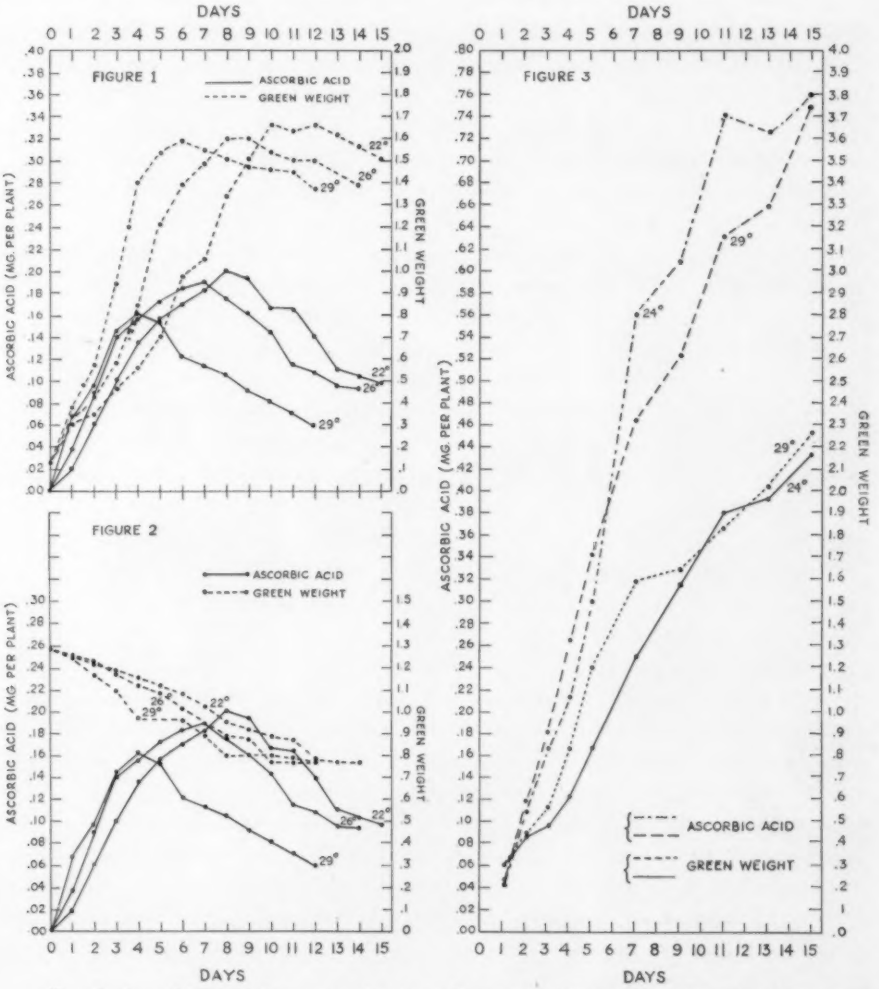


FIG. 1. Ascorbic acid (mg. per plant) and green weights (g.) of seedlings grown in darkness at different temperatures. FIG. 2. Ascorbic acid (mg. per plant) and dry weights (g. × 10) of seedlings grown in darkness at different temperatures. FIG. 3. Green weight (g.) and ascorbic acid content (mg.) of seedlings grown in light at 29° and 24° C.

Separate ascorbic acid and green weight determinations of the different organs were made. No marked differences in either the green weight or ascorbic acid values of the hypocotyls or epicotyls of seedlings grown at dif-

ferent temperatures were found. The primary leaves attained the greatest weight at 29°, but little difference was found between those grown at the other two temperatures. The maximum ascorbic acid values in the leaves of 10 seedlings was 0.59, 0.54, and 0.49 milligrams at 29, 26, and 22° respectively. In contrast, in the roots the maximum green weights were 3.1, 4.0, and 3.9 grams and the ascorbic acid values were 0.41, 0.80, and 0.77 milligrams at the high, medium, and low temperatures respectively.

The most rapid synthesis of ascorbic acid from the food reserves in the cotyledons and the most rapid depletion of the reserves as evidenced by a visible loss of plumpness and a decrease in dry weight were observed at 29°. This may be noted in the appearance of the cotyledons of five-day-old plants at each of the three temperatures as shown in figure 4.[2] The maximum ascorbic acid values were observed in the cotyledons at 29° after 24 hours, at 26° after 48 hours, thereafter decreasing in both sets. At 22° the maximum value was found after two days and was maintained at approximately the same level until the fourth day. Shedding of most of the cotyledons occurred by the sixth, eighth, and tenth days at 29, 26, and 22° respectively.

The effect of temperature on rapidity of decrease in dry weight at successive stages of development is shown in figure 2. The dry weights continued to decrease for approximately two days after the total green weights ceased to increase. During this period growth continued as measured by the increasing length of the stems (epicotyls). Loss in fresh weight of the hypocotyls at this stage was responsible for the lack of increase in total green weight. The results tend to show that the final dry weight is approximately the same in plants grown at the three temperatures, suggesting that although the rate of respiration varied, the total amount of respiration was approximately the same.

*Experiments with Plants Grown in Light.* These experiments were conducted during the winter months when carbohydrate synthesis was greatly limited by the low light intensity and also by the short daily periods of illumination. With the restricted carbohydrate supply only a slight effect on growth resulted from the addition of mineral nutrients.

Results of the tests with plants grown without added nutrients are shown in tables 1 and 2, and figure 3 shows graphically the differences in total green weight and ascorbic acid values at successive stages of development of plants grown at 24° and at 29° C. It was not possible to maintain a fairly uniform temperature at a level lower than 24° in this test. During the first two days of the experimental period the temperature was approximately 29° for the two groups of plants. Between the second and third days, following the shifting of half of the plants to a temperature of 24°, differences in the

[2] The leaves of the plants, especially those of the plant grown at 26°, became somewhat green during the time of photographing.

growth rate were observed. This was at the time the plants were beginning to emerge above the sand. It has been shown previously (Reid 1938) that the most rapid development of the mesophyll tissue and of increase in total

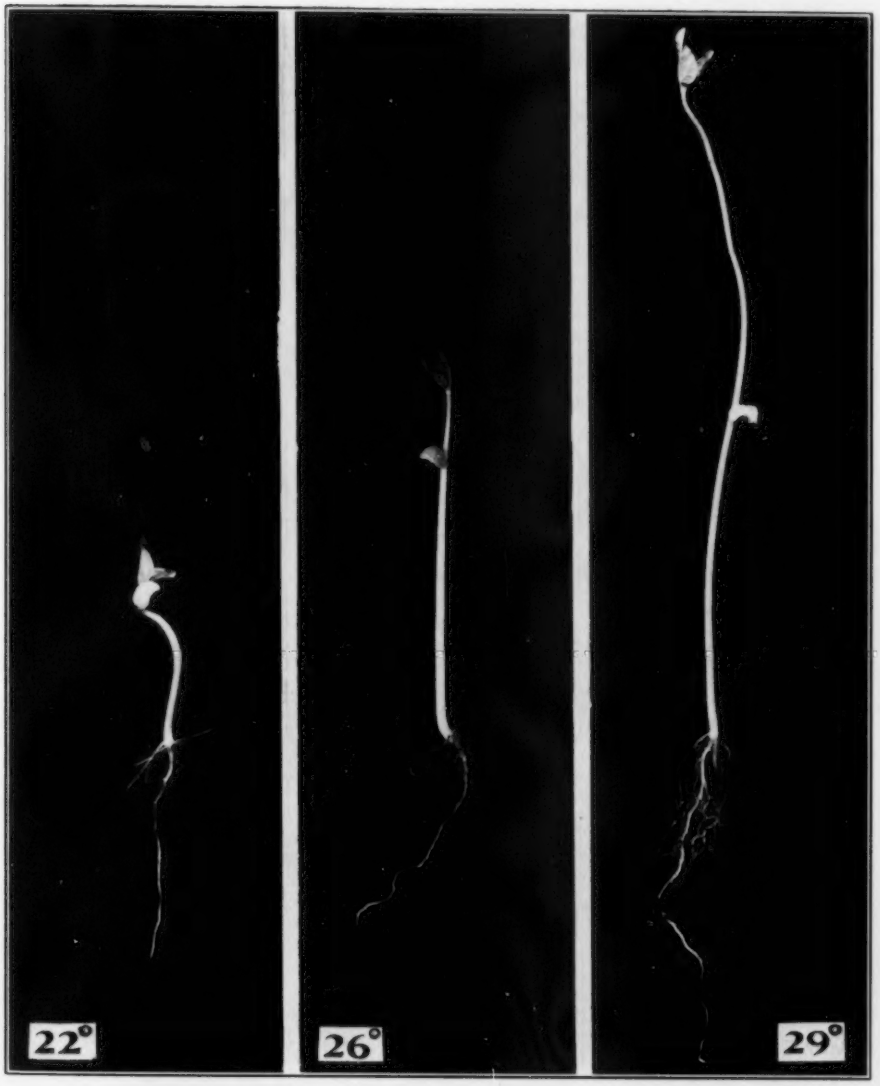


FIG. 4. Five-day-old seedlings grown in darkness at 22, 26, and 29° C.[3]

ascorbic acid in the leaves of cowpea plants grown in the light at 29° C. occurs between the third and fifth days. In the entire plant the rapid rate of gain in the total content of vitamin C continues until the sixth to the

[3] Figures 4 and 5 are published with the aid of the Lucien M. Underwood Memorial Fund.

TABLE 1

*Green weights (g.) of organs of plants grown in light, some at 29° C., others at 24° C.*

| | 29° | | | | | | 24° | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age days | Cotyledons | Hypocotyls | Roots | Primary leaves | Upper stems & compound leaves (epicotyls) | Total | Cotyledons | Hypocotyls | Roots | Primary leaves | Upper stems & compound leaves (epicotyls) | Total |
| 1 | 0.30 | 0.02 | | | ..... | 0.32 | 0.28 | 0.02 | | | ..... | 0.30 |
| 2 | 0.29 | 0.06 | 0.07 | 0.013 | ..... | 0.44 | 0.32 | 0.04 | 0.06 | 0.01 | ..... | 0.43 |
| 3 | 0.28 | 0.12 | 0.11 | 0.04 | 0.012 | 0.56 | 0.32 | 0.07 | 0.06 | 0.031 | 0.005 | 0.48 |
| 4 | 0.22 | 0.23 | 0.25 | 0.10 | 0.04 | 0.84 | 0.30 | 0.12 | 0.11 | 0.06 | 0.015 | 0.61 |
| 5 | 0.16 | 0.26 | 0.41 | 0.24 | 0.13 | 1.20 | 0.26 | 0.23 | 0.19 | 0.11 | 0.05 | 0.84 |
| 7 | 0.07 | 0.21 | 0.78 | 0.37 | 0.16 | 1.59 | 0.11 | 0.20 | 0.51 | 0.33 | 0.10 | 1.25 |
| 9 | ..... | 0.18 | 0.85 | 0.42 | 0.20 | 1.65 | 0.09 | 0.15 | 0.84 | 0.40 | 0.11 | 1.59 |
| 11 | ..... | 0.16 | 0.96 | 0.50 | 0.21 | 1.83 | ..... | 0.15 | 1.07 | 0.54 | 0.14 | 1.90 |
| 13 | ..... | 0.17 | 1.05 | 0.55 | 0.29 | 2.06 | ..... | 0.15 | 1.13 | 0.54 | 0.14 | 1.96 |
| 15 | ..... | 0.17 | 1.25 | 0.54 | 0.41 | 2.37 | ..... | 0.15 | 1.36 | 0.60 | 0.17 | 2.28 |

TABLE 2

*Total ascorbic acid (mg.) in organs of plants grown in light, some at 29° C., others at 24° C.*

| | 29° | | | | | | 24° | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age days | Cotyledons | Hypocotyls | Roots | Primary leaves | Upper stems & compound leaves (epicotyls) | Total | Cotyledons | Hypocotyls | Roots | Primary leaves | Upper stems & compound leaves (epicotyls) | Total |
| 1 | 0.032 | 0.009 | | 0.002 | ..... | 0.043 | 0.033 | 0.009 | | 0.002 | ..... | 0.044 |
| 2 | 0.055 | 0.018 | 0.019 | 0.017 | 0.003 | 0.112 | 0.074 | 0.017 | 0.015 | 0.011 | 0.001 | 0.118 |
| 3 | 0.066 | 0.028 | 0.027 | 0.054 | 0.005 | 0.180 | 0.080 | 0.029 | 0.020 | 0.033 | 0.003 | 0.165 |
| 4 | 0.050 | 0.028 | 0.059 | 0.117 | 0.010 | 0.264 | 0.075 | 0.031 | 0.033 | 0.070 | 0.006 | 0.215 |
| 5 | 0.010 | 0.014 | 0.073 | 0.230 | 0.014 | 0.341 | 0.069 | 0.030 | 0.043 | 0.140 | 0.014 | 0.296 |
| 7 | 0.006 | 0.018 | 0.159 | 0.257 | 0.025 | 0.465 | 0.027 | 0.023 | 0.129 | 0.359 | 0.024 | 0.562 |
| 9 | ..... | 0.022 | 0.162 | 0.307 | 0.033 | 0.524 | 0.010 | 0.017 | 0.237 | 0.324 | 0.022 | 0.610 |
| 11 | ..... | 0.024 | 0.219 | 0.346 | 0.045 | 0.634 | ..... | 0.020 | 0.282 | 0.420 | 0.020 | 0.742 |
| 13 | ..... | 0.024 | 0.250 | 0.326 | 0.061 | 0.661 | ..... | 0.020 | 0.286 | 0.393 | 0.028 | 0.727 |
| 15 | ..... | 0.027 | 0.235 | 0.326 | 0.162 | 0.750 | ..... | 0.023 | 0.285 | 0.422 | 0.030 | 0.760 |

seventh day. After the fourth day when the stored reserves are nearing exhaustion the gain is presumably chiefly a consequence of photosynthetic action in the mesophyll tissue. The chief effect of a lower temperature after the seedlings are about to emerge is a retardation in the rate of development of the mesophyll, and simultaneously in the rate of ascorbic acid synthesis. The differences in the rate of ascorbic acid accumulation are not so great

FIG. 5. Fifteen-day-old seedlings grown in daylight at 24 and 29° C.

as the difference in the rate of growth at the two temperatures. During the period of extensive development of mesophyll at 24° the total ascorbic acid increased until it exceeded that of the high temperature-plants. Between the thirteenth and fifteenth days the mesophyll of the first set of compound leaves developed considerably and more so at 29° than at 24°, thus causing an appreciable increase in the total content on the fifteenth day. Had the

experiment continued until the compound leaf of the 24°-plants had reached a like stage of development, the former difference in total ascorbic acid content might have again been re-established. The 24°-temperature could not be maintained after the fifteenth day, hence the experiment was terminated.

The most conspicuous difference in the appearance of the two groups of plants was the longer epicotyls and hypocotyls and finer, more flexible, and more profusely branched roots of the high temperature plants. The difference in the appearance of the plants is shown in figure 5. The roots of plants in another experiment conducted at 18–20° C. had more marked differences as compared to those of the 29°-plants than had those of the present experiment. The roots were relatively large in diameter, they were extremely brittle and not much branched. The leaves were of a distinctly paler green color than those of the high temperature-plants.

*Metabolism Experiments.* Most of these experiments were conducted during periods of relatively high light intensity, hence there was considerable growth response to fertilizers. Plants of approximately uniform size and appearance were employed. Green weight and ascorbic acid determinations were made in the afternoon preceding the test period. At the time the

TABLE 3

*Summary of results of five tests on the metabolism of ascorbic acid in seedlings kept at different temperatures*

| Plants tested in p.m. previous to being kept in darkness | | | Plants tested in a.m. following a 12- to 18-hour period in darkness | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Low temperature | | | | Higher temperatures | | | |
| Time of tests | Green weight | Ascorbic acid | Time of tests | Temp. in different tests | Green weight | Ascorbic acid | Percentage change in ascorbic acid | Temp. in different tests | Green weight | Ascorbic acid | Percentage change in ascorbic acid |
| | *g.* | *mg.* | | | *g.* | *mg.* | | | *g.* | *mg.* | |
| 5: 30 p.m. Dec. 3 | 15.40 | 5.21 | 5: 30 a.m. Dec. 4 | 13° | 14.91 | 5.23 | +0.4 | 24° | 15.61 | 4.77 | − 8 |
| 3: 00 p.m. Mar. 28 | 42.07 | 16.19 | 9: 00 a.m. Mar. 29 | 8° | 41.44 | 15.68 | −3.1 | 27° | 43.22 | 12.62 | −21 |
| 3: 00 p.m. Apr. 21 | 20.67 | 6.91 | 9: 00 a.m. Apr. 22 | 8° | 22.49 | 7.30 | +5.6 | 27° | 23.58 | 5.80 | −16 |
| 3: 00 p.m. Apr. 29 | 12.18 | 4.94 | 9: 00 a.m. Apr. 30 | 15° | 12.72 | 4.80 | −2.8 | 27° | 13.43 | 4.18 | −15 |
| 2: 00 p.m. May 6 | 18.09 | 6.15 | 8: 00 a.m. May 7 | 20° | 18.50 | 5.87 | −4.6 | 27° | 19.05 | 5.19 | −16 |

ascorbic acid assays were made, comparable cultures were placed in dark chambers kept at different temperatures. The low temperatures ranged in different tests from 8° to 20° C. and the high temperatures from 24° to 27° C. Duplicate determinations, five plants being used in each, were made of the green weights and ascorbic acid content of the different organs. In the experiments herein reported, the results were obtained with plants which received mineral nutrients.

Table 3 summarizes the results of five tests in terms of total value per plant. The results of the experiment conducted on April 29 show that there was relatively little difference in green weight (+4%) and in the ascorbic acid content (−2.8%) of plants kept for eighteen hours in darkness at 15°, whereas in those kept similarly at 27° there was a 9 per cent higher green weight and a loss of 15 per cent in total ascorbic acid.

In another experiment (March 28) in which somewhat larger and older plants were used, cultures kept for 18 hours at 8° showed no apparent gain in green weight and only a slightly lower ascorbic acid value (3.1%). Similar cultures kept at 27° appeared to gain only slightly in green weight and showed a loss of 21 per cent in total ascorbic acid. In the December 3–4 test, the plants were kept in darkness only 12 hours. The decrease in ascorbic acid in the plants kept at 27° was only about 8 per cent. The loss would probably have been somewhat greater if the plants had remained in darkness for 18 hours and also if the temperature had been kept at approximately 27° as was true in the other four tests. In all the tests the losses were found in the tops, particularly in the leaves.

## DISCUSSION

The results of these tests show that the temperature of germination influences the ascorbic acid content in cowpea seedlings with respect to the total quantity present at the different stages of development, to the maximum content, and also to the final content. The temperature which favors rapid ascorbic acid accumulation is one which also favors rapid mobilization of the stored food reserves.

There is a suggestion in these results that the temperatures which are favorable to germination, if continued for a certain length of time, may be those which also permit considerable ascorbic acid accumulation. The lack of agreement between the temperature for germination and the ascorbic acid content in different types of seedlings in Moldtmann's experiments is not surprising. The types of plants which he used are known to vary with respect to the temperature which is most favorable for germination and early growth of the seedling. Relatively low germination temperatures are generally considered best for *Avena sativa* and *Pisum sativum*, slightly higher temperatures for *Zea mays* and *Phaseolus vulgaris*, and still higher temperatures for

*Polygonum fagopyrum*. *Vicia faba* does well over a wider range of temperatures. These variations among different types of plants with respect to the influence of temperature upon germination agree fairly well with the variations in ascorbic acid accumulation at different temperatures as reported by Moldtmann. His observation that differences in temperature had marked effects on respiratory intensity but caused no change or only a slight change on ascorbic acid content during a four hour respiratory test-period in seedlings of *Vicia faba* grown at 12°, and of *Pisum sativum* grown at 25°, differs with respect to the ascorbic acid values from the present results with cowpea seedlings, and also with his own results with *Pisum* as previously mentioned. More than a very small production of ascorbic acid with four- to seven-day-old seedlings would not be expected during a four-hour test-period. In that length of time one might expect the order of change to be no greater than the experimental error. The vitamin C values which Moldtmann obtained at 35 to 40° in the respiration tests are, however, actually lower both with *Pisum* and *Vicia* than those found at 25° and 3–5° C.

In the present tests high temperatures also favored high respiratory intensity as evidenced by greater rapidity of loss in dry weight but they also caused a definite difference in ascorbic acid content,—first, a tendency to a more rapid accumulation leading, however, to a lower maximum value and later, to a greater loss. The lower maximum value found at 29° on the fourth day suggests the possibility of previous losses, that is, that the quantity found on the fourth day does not represent the entire amount which was synthesized. It is possible, however, that the lower maximum value results from a loss in content of the vitamin precursor. Nightly losses in ascorbic acid have been shown previously (Reid 1941) to occur by the sixth night in cowpea seedlings grown under normal alternations of daylight and darkness. This is the time of exhaustion of reserves stored in the cotyledons. Similar losses presumably may have occurred during the earlier phases of growth, but were not measurable because synthesis from a stored precursor was greater than the loss.

The difference in the effects of temperature on total ascorbic acid accumulation in seedlings of cereals as reported by Kuthy (1938) and Moldtmann (1939) may possibly be caused by a difference in stage of development of the plants tested. The former investigator employed ten-day old seedlings whereas the latter disregarded age, using seedlings in an early phase of development which had attained a definite size.

Similar, though more pronounced effects of high temperatures upon the ascorbic acid content of animal tissues have been observed. Martini and Torda (1937) kept guinea pigs in chambers for an hour or two at 40–46° C. and killed them after an acceleration of pulse and respiration were noted. The ascorbic acid content of the liver and adrenals was less than half and

that of the brain slightly more than half that of the controls not exposed to the heat. These investigations also found that injection of the vitamin into guinea pigs seemed to render them somewhat more resistant to the high temperature. Losses of ascorbic acid are also known to occur in the tissues of animals having fever producing-infections but it is not known definitely that the loss is a direct consequence of the increased temperature.

The results of the metabolism tests show that there tend to be losses at night at relatively high temperatures and no or only slight losses at temperatures so low as to inhibit growth and presumably respiration also. Supposedly at intermediate temperatures there would be some loss but less than at high temperatures. In the results of the May sixth experiment there is a suggestion that this is true, although tests with larger numbers of plants would be required to answer the question definitely. The results of the metabolism tests afford a possible explanation of the higher ascorbic acid content after the sixth day in the low temperature-plants grown in the light, the gain in ascorbic acid being possibly caused not so much by increased synthesis as by a slower rate of metabolic loss. It is difficult to account for the marked loss in reducing value at 20° but not at 37° C. found by Wolf (1938) in segments of detached leaves of *Bryophyllum calycinum* when kept in darkness. It would be of interest to know whether or not the respiratory rate in leaves of this type is lower at 37° than at 20°.

The effects of temperature upon the ascorbic acid content of seedlings may be said to involve relations (1) to the rate of its production from the stored food reserves, (2) to the rate of metabolic loss, and (3) to the time of emergence of the seedling above the soil. Cowpea seedlings which emerge to the light quickly, when grown under customary field conditions, can apparently tolerate a relatively high rate of loss because the early development of leaves causes them to soon become independent of stored reserves. Seedlings such as those of *Pisum* which emerge much more slowly, and especially those whose leaves develop slowly, are not favored by high temperatures during their underground phases of development. Low temperatures in *Pisum* allow synthesis of ascorbic acid and apparently tend to conserve it.

There is increasing evidence from various sources that whether or not this vitamin is of importance in relation to growth, plants do not thrive during their vegetative phase of growth except under conditions which permit an increase in their total ascorbic acid content. There is evidence also, as is here shown with cowpea plants, that in independent green plants measurable increases occur only during periods of illumination.

## SUMMARY

The rates of accumulation and disappearance of ascorbic acid, as well as the respiratory intensity and rate of growth of cowpea seedlings in darkness are successively higher at temperatures of 22, 26, and 29° C.

Differences in the total ascorbic acid content of plants grown at different temperatures are associated with differences in the amount and type of growth of different organs.

It is suggested that the lower maximum vitamin C content of seedlings grown in darkness at high temperatures may be a result of a greater metabolic loss of the vitamin or, less probably, of decreased synthesis.

Within an eighteen-hour period in darkness, appreciable losses of ascorbic acid from light-grown plants occurred only under temperature conditions which were favorable to growth.

There is a lower total ascorbic acid content of the plants grown in light at 29° as compared to 24°. Reasons are advanced to suggest that it may be chiefly a consequence of a more rapid rate of metabolic loss rather than of less rapid synthesis.

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## Literature Cited

**Kuthy, A.** 1938. Ueber die Aenderung des Gehaltes an Vitamin $B_1$ und C während der Keimung von Getreidesamen. Congr. Int. Chim. Ind. Agric. Schvéningue. Compt. Rend. **1:** 119–126.

**Martini, E. & Torda, C.** 1937. Effect of high temperature upon the ascorbic acid content of the organs of guinea pigs. Klin. Wochenschr. **16:** 1763–1764.

**Moldtmann, H. G.** 1939. Untersuchungen über den ascorbinsäuregehalt der Pflanzen in seiner Abhängigkeit von inneren und äusseren Faktoren. Planta **30:** 297–342.

**Povolockaja, K. L.** 1937a. Vitamin C in germinating seeds. Bull. Applied Botany, Genetics, Plant Breeding (U.S.S.R.) Suppl. 84, Vitamin Problems **II:** 20–57.

———. 1937b. Vitamin C in germinating seeds. Compt. Rend. (Doklady) de l'Academie des Sciences U.S.S.R. **17**(1–2): 35–38.

**Reid, Mary E.** 1941. Metabolism of ascorbic acid in cowpea plants. Bull. Torrey Club **68:** 359–371.

———. 1938. The effect of light on the accumulation of ascorbic acid in young cowpea plants. Am. Jour. Bot. **25:** 701–710.

**Wolf, J.** 1938. Ueber Schwankungen des Gehaltes an Ascorbinsäure in Abgeschnittenen Blättern von Bryophyllum Calycinum bei verschiedenen temperaturen. Planta **28:** 725–729.

# STUDIES IN THE ERICALES: A REVIEW OF THE NORTH AMERICAN GAYLUSSACIEAE; WITH REMARKS ON THE ORIGIN AND MIGRATION OF THE GROUP

W. H. Camp

## INTRODUCTION

In his Manual, Small treated the North American huckleberries as three genera different from *Gaylussacia*.[1] Shortly after, in the first of this series of Studies,[2] I questioned the advisability of these segregations primarily on the basis of our incomplete knowledge of the South American material. It has since been necessary for me to study certain species from that region in some detail. At the same time the available material of the genus was reexamined and the literature of the group brought together in greater completeness. The results of this survey are presented here.

The Gaylussacieae, a tribe of the Vacciniaceae [or if one prefers a broader phyletic interpretation, a tribe of the subfamily Vaccinioideae of the Ericaceae] is limited to the western hemisphere,[3] the greatest concentration of species being in southeastern Brazil. Since it seems apparent that the group arose in South America, where only one genus is recognized, no taxonomic segregation should be attempted until the material of that continent has first been studied, at least in some detail. So far as I can ascertain this has never been done.

The more common and widespread of the North American Gaylussacieae were, for the most part, described first as species of *Vaccinium*. We therefore find that the earliest literature dealing with them as a group was primarily concerned with their separation from this genus rather than from the South American type of *Gaylussacia*. Although *Gaylussacia* was described in 1818 on the basis of Colombian and Venezuelan material, it was not until 1841 that the North American forms now placed in the tribe were suspected as being fundamentally different from *Vaccinium*.[4] The group was then given the provisional name *Decachaena* T. & G. The same year Nuttall presented a paper in which the North American material known to him was held as separate from both *Gaylussacia* and *Vaccinium*, the emphasis being placed on its difference from the latter genus. In this paper,[5] pub-

[1] Small, J. K., Manual of the Southeastern Flora, pp. 1007–1010, 1506. 1933.

[2] Camp, W. H., Bull. Torrey Club **62**: 129–132. 1935.

[3] The Bornean *Rigiolepis*, sometimes placed in the Gaylussacieae, seems to have closer affinities with the Vaccinieae.

[4] Gray, Asa. Am. Jour. Sci. **42**: 43. 1841. The same note may be found in Gray, Asa. Lond. Jour. Bot. **3**: 234. 1844.

[5] Nuttall, T. Trans. Am. Phil. Soc. II. **8**: 259–261. 1842. Although the date of this publication is generally given as 1843, there is evidence that the part containing the above cited pages appeared in December, 1842.

lished in 1842, he proposed the name *Decamerium* for the group. The following year Torrey[6] placed those species with which he was concerned in *Gaylussacia*. And, except for a brief and abortive nomenclatural excursion led by Kuntze[7] into *Adnaria*, they remained there until 1931. Finding that he could make some new nomenclatural combinations, Ashe[8] in that year revived the name *Decamerium* and dumped into it all the North American species which, because they were either misunderstood or unknown to him, had not been included by Nuttall. Two years later Small (*l.c.*) resurrected *Decachaena*, placed part of the North American species under it and erected two additional genera for the remainder.

If we take up the problem of *Decachaena* T. & G. (1841) vs. *Decamerium* Nutt. (1842), there is little argument. The brief and informal discussion by Gray in a footnote (*l.c.* 1841), wherein he refers to it as "*Decachaena Torr. et Gray ined.*," can scarcely be taken as a valid description, even though there is a reasonably clear outline of the diagnostic characters of the group separating it from *Vaccinium* as well as mention of the type and additional species which he intended it to contain. Ashe's note (*l.c.* p. 197) where he states that "the name [*Decachaena*] apparently was given only a subgeneric significance" is obviously incorrect, otherwise both Torrey (*l.c.*) and Gray[9] would not have listed it as a synonym of *Gaylussacia* coequal with *Decamerium* Nutt. The important fact is that Gray did not give us a formal description of *Decachaena* in 1841 and, before he could, Nuttall had already published his *Decamerium*. Its status, therefore, is only that of a nomen and should have given way to *Decamerium* in Small's treatment. However, *Decachaena* is available as a subgenus or section and, although applied too broadly, has already been used as such by Drude.[10]

## THE SOUTH AMERICAN SPECIES

Before we become lost in a discussion of the less interesting but necessary nomenclatural history of the group, let us turn to the material representative of the bulk of the tribe—to the South American species.

It is not my intention to treat the South American material in anything approaching a satisfactory manner either in this place or in the immediate

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[6] Torrey, John. Fl. N. Y. 1: 448–449. 1843.

[7] Kuntze (Rev. Gen. 1891) transferred forty-eight vacciniaceous plants—mainly of the genus *Gaylussacia*—into *Adnaria* Raf. My conclusion that *Adnaria* does not belong in the Vacciniaceae but in the Styracaceae is discussed in a paper now in press (CASTANEA) under the title "Studies in the Ericales: The Search for *Adnaria odorata* Raf., and *Arbutus obtusifolius* Raf." Since *Adnaria* Raf. (1817) properly belongs to the Styracaceae the conservation of *Gaylussacia* H.B.K. (1818) over it was unnecessary.

[The paper mentioned above has since appeared; Castanea 6: 80–83. 1941.]

[8] Ashe, W. W. Rhodora 33: 197–198. 1931.

[9] Gray, Asa. Synop. Fl. N. A. Ed. I. 1878; Ed. 2. 1886.

[10] Drude, O., *in* Engl.-Prantl, Nat. Pflfam. 4[1]: 50. 1889.

future. The assembling of material adequate for a definitive taxonomic treatment is impossible at the present time. The genus is poorly collected, many of the species being known only from the types or from a few scattered examples; the area wherein we find the greatest concentration of described species is in need of considerably more botanical exploration; and, because of the complicated and interlocked variabilities of the collections now before me, it is obvious that a personal knowledge of the plants in the field would be most desirable. But, even so, there is sufficient material at hand to give us a reasonably clear picture of the genic reaction-pattern of the group.

Characteristically, the South American members of the Gaylussacieae are small or medium-sized shrubs, often with underground rhizomes, and with relatively small, persistent and often pubescent leaves. The majority of the species bear gland-hairs on various of the organs, a common trait of the Ericales; and the inflorescence is generally racemose, often with persistent leafy bracts.

When one examines this material, it is apparent that evolution has progressed along several lines. The leaves may have become reduced, particularly in width, often with their margins revolute, and they sometimes may be essentially glabrous. The gland-hairs have evolved into two general types: (1) clavate-stipitate structures, their filiform bases varying considerably in length, the glandular portion with no visible pellicle, and (2) capitate, subsessile glands with an obvious pellicle. There also appear to be forms transitional between these two gland types. It is also apparent that several of the lines have given rise to forms which rarely bear glands of either type except perhaps for a few scattered on the inflorescence or along the leaf margins or, on occasion, these may be lacking. In the more highly evolved forms the primitive, persistent, leafy bracts of the inflorescence may be reduced to mere bracteoles and become early-caducous. In these forms it is not unusual for the racemes also to be reduced. The flowers, although varying considerably from species to species, do not seem to show any basically different structures. It is certainly evident that the inflorescence patterns and flower structures of the South American forms do not exhibit the wide diversity found within the genus *Vaccinium* (sensu lato).

In my examination of the available South American material I have noted the presence of relatively well marked sections or species-groups, particularly toward the ends of the several lines of evolution where marked divergences in habit and structure are obvious. Yet, when the group is viewed as a whole, these lines seem to become tangled in a common plexus so that, for the present at least, I am at a loss to find any combination of characters which would serve to separate them into clearly defined or easily separable units of more than subgeneric rank. But this statement is made with certain reservations, for I have as yet made no attempt to compare the

correlated leaf, gland, and inflorescence types and corolla forms, either with the known differences in anther-filament ratios (which may be merely a function of corolla length) or the differences in pubescence of the filaments; and, what is more important, I have been unable to re-examine in any completeness the carpel morphology of the various South American species. This last task will be essential in a definitive study of the group, and might serve to exclude from the tribe certain of those forms which appear to be peculiarly aberrant.

Briefly, then, with specimens of a reasonable majority of the South American Gaylussacieae before me, I am unable to discern any points of difference of sufficient magnitude which, for the present, would lead me to separate the group into segregate genera coequal with *Gaylussacia* as typified by *G. buxifolia* H.B.K. However, sectional and subsectional units may be recognized, if only for convenience in systematic treatment.

## THE RELATIONSHIPS OF THE NORTH AMERICAN SPECIES

It is to be admitted without argument, if one deals solely with the North American species, that they fall into three very well marked groups. Furthermore, these groups are so distinct in their general appearance and detailed morphological characters that one readily suspects that they have had separate origins and represent different kinds—or genera—of plants. It is obvious that Small came to this conclusion while preparing his 1933 Manual. And it is to be admitted that I, too, at times in my general writings and remarks, have been swayed toward this viewpoint, being too much influenced by the "weight of authority."

Small (Man. p. 1007) left no doubt that he considered the North American material to be different from the South American for he says: "This [*Decachaena*] and the two following genera [*Lasiococcus* and *Buxella*] are often included in *Gaylussacia* which, however, technically considered, forms a group of plants confined mostly to northern South America." Small had ample precedent for keeping the North American and South American forms separate, for we find the North American material treated by previous authors as follows:

Nuttall (*l.c.* 1842)—*Decamerium.*
Hooker f.[11] (1876)—*Gaylussacia* Sect. *Decamerium;* and Sect. *Vitis-idaea* (= *Buxella* Small).
Drude (*l.c.* 1889)—*Gaylussacia* Subgen. *Decachaena;* and Subgen. *Pseudo-Idaea* (= *Buxella* Small).
Ashe (*l.c.* 1931)—*Decamerium.*

In the foregoing list, it is interesting to note that the two students of our local flora—Nuttall and Ashe—applied a single generic name to all our

[11] Hooker f., *in* Benth. and Hook. f. Gen. Pl. 2: 573. 1876.

North American material, keeping it separate from *Gaylussacia;* whereas the systematists—Hooker and Drude—recognized two sections or subgenera, but kept these separate from the South American *Eulussacia* (Hooker as a section, Drude as a subgenus). And as further corroboration of this view that the North American and South American Gaylussacieae are separable, Sleumer,[12] in his current systema of the Vaccinioideae (as a subfamily of the Ericaceae) treats the Gaylussacieae as a tribe consisting of the single genus *Gaylussacia,* but having in it the following three divisions:

Sect. I. *Decachaena*—all North American species except one.
Sect. II. *Vitis-idaea*—the North American *G. brachycera* (Michx.) Gray.
Sect. III. *Eulussacia*—all South American species.

Thus, for a century, the continuity of the concept that the North American Gaylussacieae are phyletically separate from those of South America has been maintained.

Let us now briefly examine the North American genera as defined by Small and see in what manner—and "technically considered"—they differ from the general pattern of the South American group. We shall first consider *Lasiococcus.*

As defined by Small, the genus *Lasiococcus* consists of three species: *L. dumosus,* a species of the Coastal Plain from Louisiana to Florida and northward to Newfoundland; *L. Mosieri,* locally abundant on the Coastal Plain mainly in Florida and from there to Louisiana; and *L. orocola,* known from a single locality in North Carolina.

Small's descriptions are, with one exception, ample. He has not mentioned the type of gland-hair characteristically present on the leaf, the inflorescence, and hypanthium (or in maturity, the fruit). In this group of species the glands are clavate-stipitate and do not have an obvious secretion-pellicle.

If we now consider *L. Mosieri* and compare it with certain Brazilian species (e.g. *Gaylussacia pseudogaultheria* Cham. & Schlecht.; *G. hispidula* Meissn.) we note a great similarity. In fact, I have specimens of *Lasiococcus Mosieri* before me which I cannot easily separate from individuals of *Gaylussacia pseudogaultheria,* a species known from the States of Paraná, Minas Geraes, etc.[13] It is also obvious that these species are part of a complex

[12] Sleumer, H. Vaccinioideen-Studien. Bot. Jahrb. (Sond.-Abdr.) **71**: 375–510. 1941.

[13] The question will immediately arise as to why I do not here place *L. Mosieri* in synonymy under *G. pseudogaultheria.* I have not done so solely for the reason that the specimens of both species before me exhibit certain variations which must be considered only in the light of the type of the Brazilian form, which I do not have. The decision whether *G. pseudogaultheria* should be broadly defined so as to include *L. Mosieri,* or whether it should be rigidly delimited into two groups, so that *L. Mosieri* would include part of what is now considered to be *G. pseudogaultheria,* must wait for a definitive treatment of the group and a comparison of the types of both. It is sufficient only to point out at the present time that I am unable to separate certain forms from Florida and Brazil into different species.

related via *G. amazonica* Huber of the Amazonian low-land *campos* and *G. cacauminis* A. C. Smith of Mt. Duida (Venezuela) to *G. buxifolia* H.B.K., a Venezuelan and Colombian species, the type of the genus.

It is also worth recalling that, on a recent trip to the southeastern Coastal Plain (March, 1941), I noted that *L. dumosus* had persistent leaves, at least northward into North Carolina. In Florida, *L. Mosieri* often retains its leaves in a living condition throughout the winter and well into the next season, at least until the flowers are present and the new set of leaves is well developed. Persistent leaves are, of course, characteristic of the South American members of the tribe.

So far as the general pattern of the plant is concerned *L. orocola* appears to occupy a position somewhat intermediate between *L. dumosus* and *L. Mosieri*. If the material had come from the Coastal Plain it might be thought to be only an intergrade form. However, its presence in only one place, and this an isolated, high-altitude, swampy area near Flat Rock, Henderson Co., North Carolina—in the general region of the Blue Ridge which I recognize as being rich in archetype ericaceous species—leads me to suspect that this species or its immediate ancestor may have been introduced into North America in remote times and that this single known locality represents a marked restriction of a once much wider range. It should be sought for further in similar areas in the Southern Appalachians and Inner Piedmont. Because of the accumulation of morphological reductions characteristic of the species, it is obvious that, within its group, the more northerly ranging *L. dumosus* is a derived form.

In the absence of any cytological data, no phyletic sequence will be given for these three species. It is to be noted here only that these three North American forms, segregated by Small into the genus *Lasiococcus*, are closely related and have the same plant habit, inflorescence type, stipitate glands, etc., characteristic of a group of South American species of *Gaylussacia* of which one is the type of the genus. Furthermore, if *Lasiococcus* Small (1933) could be held as separate from *Gaylussacia* the name would have been an unfortunate choice, being confusable with the previously described *Lasiococca* Hook. f. (1887), one of the minor genera of Oriental Euphorbiaceae.

Our next group for consideration is *Decachaena* (sensu Small non Gray). Here I recognize five species. These differ from the foregoing group by having capitate, subsessile glands which, at maturity, exhibit a well-marked pellicle filled with secreted resinous substances[14] as well as additional (but

[14] In many instances, as on mature organs under natural conditions or on herbarium material, these globules have collapsed by rupture of the pellicle, leaving the resinous "spots" characteristic of the group, together with the remnants of the secretion cells. In the foregoing group of species, the stipitate glands either contain the oil within the cells or secrete it on their surfaces without the formation of a notably distended pellicle. Because of their differences in viscosity, adhesiveness and drying qualities, it is my opinion that the basic compounds secreted in the two groups may be chemically dissimilar.

not constant) differences in habit, leaf form, inflorescence pattern and flower shape.

Of the three "sections" or species-groups previously recognized by me in the North American members of this group (Camp, *l.c.*)—in the present paper called subsections—it is to be noted that one, the *Baccatae,* has the resinous glands on both the upper and lower surfaces of the leaf, although they are much better developed on the latter. Both the *Ursinae* and *Frondosae* have these glands limited to the lower surface.

Of the five species in this series, three (*G. baccata, G. nana* and *G. tomentosa*) have much the same general habit, being smallish shrubs much given to the formation of extensive clones. Conversely, the remaining two (*G. frondosa* and *G. ursina*) are generally taller plants (particularly *G. frondosa,* which may sometimes reach 3 meters), neither of which form the extensive, matted clones characteristic of the previous three, although they do spread to a certain extent by means of rhizomes.

It was only natural for Gray when he described the entities *nana* and *tomentosa* to consider them merely as varieties of *G. frondosa,* a plant with which he was personally familiar. Their smaller stature would also lead one to the conclusion that they were only variants (possibly due to habitat) of the more widespread species. It is dangerous to extrapolate one's information too far, yet unpublished data available to me gives clear evidence that the archetype, diploid species of *Vaccinium* are, for the most part, low forms spreading extensively by underground rhizomes, whereas their tetraploid derivatives invariably are coarser plants and generally less given to the formation of extensive clones. As a further extension of this general principle, certain of the derived hexaploid forms may, in favorable situations, reach a height of 8 meters, often being compact monopodial shrubs.

If the Gaylussacieae follow the general pattern of the Vaccinieae (which seems quite likely) we therefore should be wary of considering the entities *nana* and *tomentosa* merely as varieties of *G. frondosa;* rather, it is more likely that the wide-ranging *G. frondosa* has been derived from one (possibly *nana*) or even by allopolyploidy from a combination of both. For this reason, and until the cytological picture of the group is known, I prefer to treat these three as distinct entities of specific rank. *G. baccata* is, incidentally, known to be a diploid species and is isolated from those forms which I suspect are diploids by differences in ecological preferences; at least its range is different.

If we turn our attention once more to the South American material, it is obvious that subsessile glands with pelliculate membranes are characteristic of another group of species (e.g. *G. octosperma* Gardn., *G. ledifolia* Mart., *G. Chamissonis* Meissn., *G. pallida* Cham., *G. thymelaeoides* Meissn.,

etc.),[15] apparently abundant in eastern Brazil. Regardless of the ultimate nomenclatural disposition of these forms, it is sufficient only to point out that the gland type characteristic of a group of species in North America is also found in a series of South American forms of *Gaylussacia*. In turn, a few of these do not appear to have the pellicle so well developed as in the North American species and seem, in part, to connect with additional forms indicating transition stages between this gland type and that characteristic of the more primitive—and typical—species of the genus. In habit, these South American species have much in common with the low-growing forms previously noted from North America. Of the South American species (e.g. *G. octosperma* Gardn., or at least *Glaziou 16229* from the Organ Mountains and so labeled), a few have abundant and large glands on the lower leaf surface and almost none on the upper, a condition similar to that in the subsections *Frondosae* and *Ursinae;* whereas others of them have the glands on both surfaces as in the subsection *Baccatae*.

Admittedly, the South American species here listed have smaller and, in general, more indurated leaves than those in North America with which they seem to be most closely related. But if we take these South American forms and place them at one end of a series and *G. ursina*—the coarse and thin-leafed species now limited to the Southern Appalachians—at the other end, we will immediately note that *G. baccata*, *G. tomentosa* and *G. nana* occupy their respective niches in intermediate positions in the plexus of forms bearing pelliculate glands here under discussion.

It is therefore obvious that the group of North American species placed by Small in *Decachaena* cannot, except on the flimsiest of characters, be held separate from South American forms which lie well within the present definition of the genus *Gaylussacia*.

We now come to the last of Small's three genera of North American huckleberries, composed of the monotypic *Buxella brachycera*. There is little to add to Wherry's excellent account[16] of the history of our knowledge of this interesting plant. Among our North American huckleberries it is certainly the best marked species on account of its heavily indurated evergreen leaves, devoid of glands on either surface. The living plant has much the aspect of certain species of *Vaccinium* and its inflorescence pattern, flower and fruit conformation serve only to heighten the illusion. In fact (and again on the basis of the North American material only) it would certainly appear to merit generic rank, the carpel morphology being the only character which gives us a clue to its relationships.

[15] It is to be remembered that I make no warranty as to the correct application of these names, some of which may be synonyms of earlier species. They are names which are associated with important South American collections, in some instances the types, now before me and which must stand or fall only in the light of a future and much needed revision of the genus.

[16] Wherry, E. T. Bull. Torrey Club **61**: 81–84. 1934.

But in our examination of the South American material from Brazil we come upon such things as *Gaylussacia Riedelii* Meissn., and *G. salicifolia* Cham. & Schlecht., with heavily indurated and obviously evergreen leaves, their margins coarsely toothed (as are those of *Buxella brachycera*) and apparently devoid of any glands. They also have the longitudinally grooved bark (in dried material) so characteristic of *B. brachycera*. To be sure, they are coarser plants and, on occasion, may bear glands in the inflorescence, these being sometimes limited to the hypanthium. But if the Brazilian species mentioned above are not exact matches for our own plant, we have to look only to additional forms in the general region of species-concentration in eastern Brazil to find those which, on one extreme, match our plant in habit, being low, cespitose clone-formers and, again, other species completely devoid of any type of gland.

Briefly, then, had the plant for which Small erected the genus *Buxella* come from Brazil rather than from North America, it never would have been thought of as anything except a species of *Gaylussacia*. Furthermore, if Small's *Buxella* did not already have phyletic unsoundness, it certainly would have nomenclatural troubles. *Buxella* Small (1933) was already preoccupied by *Buxella* Van Tieghem (1897), a genus to which several species of Euphorbiaceae (sensu lato) from Africa and Madagascar had been referred.

## CHECK LIST AND SYNOPSIS OF THE SPECIES OF GAYLUSSACIA IN NORTH AMERICA

Because of certain minor errors of citation in the literature and omissions from important bibliographic sources, as well as for the use of those preparing manuals, local notes, etc., it is thought best to list here, together with the basic and most common synonyms, the North American species of *Gaylussacia* as I understand them at the present time. The various described subspecific entities have been omitted. They will be taken up at another time following a more definitive (and it is hoped genetic) analysis of the group, together with a complete synonymy. Their inclusion in this place is thought to be unnecessary.

GAYLUSSACIA H.B.K. Nov. Gen. Sp. Pl. **3**: 275. *t. 257*. 1818. ("nom. conserv.;" see footnote 7).

(A) Plants, especially the leaf surfaces, bearing clavate-stipiate gland-hairs, their glandular portion with no visible secretion pellicle.

Section I. *Eulussacia* Hook. f.; Benth. & Hook. f. Gen. Pl. **2**: 573. 1876. (Sensu speciei typicae generis, non auctorum variorum.)

1. G. MOSIERI Small, Torreya **27**: 36. 1927. *Lasiococcus* Mosieri Small, Man. SE. Fl. 1009. 1933. *G. Mosieri* Camp, Bull. Torrey Club **62**: 132. 1935 (comb. superflua).

2. G. OROCOLA (Small) Camp, Bull. Torrey Club **62**: 132. 1935. *Lasiococcus orocola* Small, Man. SE. Fl. 1009. 1933.

3. G. DUMOSA (Andr.) A. Gray, Chlor. Bor. Am. 50. 1846. *Vaccinium dumosum* Andr. Bot. Rep. **2**: *pl. 112.* 1800. *Vaccinium hirtellum* Ait. f. Hort. Kew, Ed. 2, **2**: 357. 1811. *Lasiococcus dumosus* Small, Man. SE. Fl. 1008. 1933.

(A′) Plants, especially the leaves, bearing capitate subsessile glands with an obviously inflated pellicle.

Section II. *Decachaena* (Torr. & Gray) Sleumer, Bot. Jahrb. (Sond.-Abdr.) **71**: 383. 1941. (Sensu speciei typicae, non auctorum variorum. Ea est *Vaccinium resinosum* Ait.)

(B) Leaves glandular on both surfaces.

Subsection *Baccatae.*

4. G. BACCATA (Wang.) K. Koch, Dendr. **2**: 93. 1872. *Andromeda baccata* Wang. Beitr. 111. *pl. 30, f. 69.* 1787. *Vaccinium resinosum* Ait. Hort. Kew **2**: 12. 1789. *G. resinosa* T. & G.; Torr. Fl. N. Y. **1**: 449. 1843. *Decachaena baccata* Small, Man. SE. Fl. 1008. 1933.

(B′) Leaves glandular only on the lower surface.

(C) Leaf apices acute to acuminate.

Subsection *Ursinae.*

5. G. URSINA (M. A. Curtis) T. & G.; Gray, Chlor. Bor. Am. 49, *t. 10.* 1846. *Vaccinium ursinum* M. A. Curtis, Am. Jour. Sci. **44**: 82. 1842. *Decachaena ursina* Small, Man. SE. Fl. 1008. 1933.

(C′) Leaf apices rounded to obtuse.

Subsection *Frondosae.*

6. G. TOMENTOSA (Gray) Small, Bull. Torrey Club **24**: 443. 1897. *G. frondosa* var. *tomentosa* Gray, Syn. Fl. N. A. Ed. I. **2**[1]: 19. 1878. *Vaccinium tomentosum,* Pursh; Gray, Syn. Fl. N. A. Ed. I. **2**[1]: 19. 1878 (as synonym). *G. tomentosa* Pursh, ex. Gray; Small, Bull. Torrey Club **24**: 443. 1897 (in synonymy, combination in error). *G. tomentosa* (Pursh) Chapm.; Small, Fl. SE. U.S. 892. 1903 (in error). *Decachaena tomentosa* Small, Man. SE. Fl. 1007. 1933. *G. tomentosa* Small; Small, Man. SE. Fl. 1007. 1933 (as synonym).

7. G. NANA (A. Gray) Small, Bull. Torrey Club **24**: 443. 1897. *G. frondosa* var. *nana* A. Gray, Syn. Fl. N. A. Ed. 2. **2**[1]: suppl. 396. 1886. *Decachaena nana* Small, Man. SE. Fl. 1008. 1933.

8. G. FRONDOSA (L.) T. & G.; Torr. Fl. N. Y. **1**: 449. 1843. *Vaccinium frondosum* L. Sp. Pl. 351. 1753. *Decachaena frondosa* Small, Man. SE. Fl. 1007. 1933.

(A″) Plants eglandular.

Section III. *Vitis-idaea* Hook. f.; Benth. & Hook. f. Gen. Pl. **2**: 573. 1876.

9. G. BRACHYCERA (Michx.) A. Gray, Chlor. Bor. Am. 54. 1846. *Vaccinium brachycerum* Michx. Fl. Bor. Am. **1**: 234. 1803. *Vaccinium buxi-*

*folium* Salisb. Parad. Lond. *pl. 4.* 1805. *Buxella brachycera* Small, Man. SE. Fl. 1009. 1933.

### A NOTE ON THE AUTHORITY FOR THE COMBINATION: GAYLUSSACIA TOMENTOSA

It is possible that future questions may arise concerning my choice of authority for the combination *G. tomentosa.* For this reason a discussion of the situation is here included.

The first use of the epithet *tomentosa* was as a variety of *G. frondosa* by Gray in 1878. (For complete citations, the foregoing synonymy may be consulted). In the same place, Gray listed the source of his name as "*Vaccinium tomentosum*, Pursh, ined." There is no evidence that Pursh ever published a description of this entity, so we must conclude that Gray got the name either from some correspondence, or from a name appended to an herbarium sheet. In 1897, in a study of the genus *Gaylussacia* in the Southern States, Small headed the paragraph discussing this plant as *Gaylussacia tomentosa* Pursh, listing the original *Gaylussacia frondosa* var. *tomentosa* A. Gray as a synonym as well as "*Gaylussacia tomentosa* Pursh," but credited this last as being published by Gray "as synonym" in the same place as the original description of the variety. This was obviously an error on Small's part, for Gray had listed it as "*Vaccinium tomentosum*, Pursh, ined."

Apparently realizing this error, Small in his 1903 Flora assigned this combination to Chapman. This was repeated in the 1913 edition. I have searched through all of the editions and as many of the various printings of Chapman's Floras as are available, as well as his few writings outside of these, and have been unable to locate any such combination, or any mention of the name even as a variety, and am forced to the conclusion that this was a further error on Small's part.

In 1933, in his Manual, Small resurrected the invalid genus *Decachaena* and made the combination *D. tomentosa*, listing *G. tomentosa* Small as a synonym. This, I think, can be taken as clear evidence that by 1933 Small realized his *G. tomentosa* Pursh ex Gray of 1897 and his *G. tomentosa* (Pursh) Chapman of 1903 were both in error.

It is my opinion that, since Pursh never gave us a description of the plant, mention of the authority for the name by Gray in synonymy as "Pursh, ined." does not constitute valid publication and that Gray should be credited with having first published the name as a taxonomic entity. Furthermore, even if he did assign the combination *G. tomentosa* first to Pursh and later to Chapman, it was Small himself who, apparently by accident, made the combination in 1897. It is therefore my conclusion that the authority for the combination should be: *Gaylussacia tomentosa* (Gray) Small.

It is to be further noted that, although the combination *Gaylussacia tomentosa* has been in common use in American botanical literature since 1897, I find no record of it either in the Index Kewensis and its Supplements or in the "Card Index of Genera, Species and Varieties of American Plants, 1885 to date"—this last commonly called the "Gray Herbarium Cards." This omission can scarcely be blamed on the editors of these indexes, for when the combination was made it was done in such a manner as to lead those who collate these invaluable bibliographic services to the conclusion that it was one which surely must have been listed previously.

## THE NORTHWARD MIGRATION OF GAYLUSSACIA

*The problem of origin and dispersal.* It is with a certain temerity that I discuss the broader aspects of the distribution of the genus *Gaylussacia* in this place and prior to a much needed taxonomic revision of the genus. Yet I cannot forego the opportunity of remarking upon the close affinity of certain of our North American plant-groups with those of South America, and the need to consider them before we attempt any segregations in our own. Too often, a familiar group, when examined solely in the light of knowledge based upon a restricted area, tends to lead one into the pitfall of a hasty and misguided taxonomic segregation; whereas, if the group as a whole is studied it may be seen that the apparently separable local material represents only the end-products of a series of evolutionary lines stemming out of a common plexus. The North American huckleberries certainly illustrate this point.

If one follows Sleumer's latest systema (which we trust is only tentative) and puts all the South American members of *Gaylussacia* into a single subgeneric group, it is obvious that the genus becomes (if there is such a thing) monosectional, for the remaining sections—including only the North American species—are much less variable, have close relatives there and should be placed with parallel material now in the supposedly wholly South American Section *Eulussacia*. Where the material warrants and exhibits even habital differences it is sometimes advisable to make regional divisions for the convenience of easier key construction. But to make phyletic divisions solely on a geographic basis sometimes leads to an absurdity, such as finding two forms as those going under the names *G. Mosieri* and *G. pseudogaultheria* placed in different sections, or even genera—forms between which I can scarcely discern varietal differences.

This close affinity of our North American huckleberries with those of South America needs to be considered rather carefully from the standpoint of plant migration. Of course, birds can always be used to explain apparently unusual distributions. It is true that birds do eat huckleberries, and this is probably their major method of dispersal. But it is approximately four

thousand miles between the northernmost known plant of *G. pseudogaultheria* and the southernmost plant of *G. Mosieri*, its scarcely separable relative. And that, to me at least, would seem to be an unusually long non-stop flight for most of our frugivorous birds. Furthermore, even greater distances separate the other North American species from their South American relatives. Therefore, our problem is to reconstruct a picture of the paleogeography of the area bounded by the outlying members of the genus; to ascertain, if possible, where they might have had their origin and whether they migrated from that area in a normal manner by gradual steps across existing land (or at most across short distances of water), or whether we will be forced to the conclusion that some unusual type of dispersal has been operative in the dissemination of the group.

*Historical backgrounds of the present distribution in South America.* The genus *Gaylussacia* has three centers of concentration, the primary being in eastern Brazil, where we find about forty species. Two secondary centers are found, one in northwestern South America from northern Peru to Colombia (with minor outliers in Venezuela); the other is in eastern North America. Both of these last mentioned areas have the same number of recorded species (i.e. 9, with the exact number for South America being less certain than for North America).

I cannot here go into a lengthy discussion of old land areas and their relation to centers of plant dispersal, but the correlation between the present distribution of *Gaylussacia* and certain land masses known to have been emergent for a long time is so close that to speculate on the dispersal of the genus requires a brief consideration of these areas and the possibility of their former connection.

In the geological part of this discussion I make no pretense of any great originality, but have drawn freely from the writings of Schuchert,[17] Branner,[18] James,[19] Tate,[20] Hitchcock,[21] and others. However, not being a professional geologist or geographer, I have had no great hesitancy in making certain generalizations from which, otherwise, I might be restrained, especially where the known facts of phytogeography would seem to warrant such conclusions.

As nearly as I can ascertain there are today in South America five areas of varying size whose surface rocks give evidence of great antiquity: (1)

[17] Schuchert, Charles. Historical Geology of the Antillean-Caribbean Region. Pp. 811. John Wiley & Sons, Inc. New York. 1935.

[18] Branner, John Casper. Bull. Geol. Soc. Am. **30**: 189–338. Map. 1919.

[19] James, Preston E. Ann. Assoc. Am. Geog. **33**: 165–193. 1933.

[20] Tate, G. H. H. Geog. Rev. **28**: 452–475. 1938.

[21] Hitchcock, C. B. (Cerro Duida and the Guayana Highlands), *in* Gleason, H. A. Bull. Torrey Club. **58**: 284–287. 1931.

Southern Chile and parts of Patagonia. (2) Portions of the mountains of eastern Brazil. (3) The Choco borderland, which probably extended from Colombia southward into Ecuador and which today has on its eastern rim the Cordillera Occidental. This borderland, which once must have extended westward into what is now the Pacific Ocean, and which has on it by far the oldest of the three northern Andean chains, may once have had connection southward with the Chilean-Patagonian mass. (4) The Santa Marta massif in northern Colombia. (5) The "Guayana Shield" having in its center the Sierra Parima and the much more publicised Sierra Pacaraima and their floristically dramatic outliers (Roraima, Duida, Auyantepui, etc.). To these areas, one ought, perhaps, add "Paria," the now nearly defunct "southern frame of the Caribbean Mediterranean," a land which, according to Schuchert, lay athwart northern South America during the Paleozoic and probably the earlier Mesozoic.

It would seem probable that, throughout the later Paleozoic and the early and middle Mesozoic, much of South America was emergent and colonizable by land plants. With the advent of the Cretaceous, the surface of South America underwent a drastic change, for large areas of it were inundated by marine transgressions. But, even so, certain upland areas remained—islands on which such land plants as were present could have been preserved during those times. As nearly as I can ascertain, these areas were: certain portions of the present mountain systems of eastern Brazil, the Chilean-Patagonian mass, the one remaining rim of the Choco borderland, and possibly the center of the Santa Marta massif. It is altogether probable that additional smaller island areas may have existed.

The Guayana Shield as now interpreted, an area stretching from the present Andes to the Atlantic and from the Orinoco southward nearly to the Amazon, is a special problem. It is the opinion of Schuchert, Tate, and Hitchcock (*l.c.*, and based in part on the work of Liddle on Roraima) that the sandstone which makes up the massive table-mountains in the central portion of the Guayana Shield was deposited during the Lower Cretaceous. It is the opinion of Hitchcock (*l.c.*, p. 285) that the peaks of the Parima Range are made up of igneous or metamorphic rock—this opinion being based on their contours as viewed from the top of Duida. It is therefore possible that the center of the Guayana Shield—the Sierra Parima—may also have been emergent during the Lower Cretaceous and an additional center of refuge for land plants in South America during that time. One thing, however, is certain. If the massive sandstone layer on much of the Guayana Shield was laid down as recently as the Lower Cretaceous (and it may be much older), the central portion of the area has been continuously emergent at least since that time and colonizable by an upland vegetation.

So far as our immediate problem—the genus *Gaylussacia*—is concerned, we have already noted that its greatest concentration of species is in eastern Brazil. Its principal center of development, therefore, is on and around one of these anciently emergent areas. The other South American center is on the rim of the equally ancient Choco borderland. After what must have been an extremely old primary dispersal, a few forms have migrated into the younger (Upper- and post-Cretaceous) Andes of Colombia and Venezuela and onto the Amazonian *campos*, one species only as yet being known from the center of the Guayana Shield, although this last area is otherwise relatively rich in ericaceous material. From its concentration in areas known to have been long emergent and its apparent scarcity on those of later age, it would seem likely that the pattern of genetic variability of *Gaylussacia* was already well defined and the genus widely dispersed in South America in Cretaceous time.

*The migration across Antillia.* If *Gaylussacia* were confined to South America the problem of its dispersal would not be so complex, but the genus has nine species in eastern North America. As has been previously pointed out—and contrary to traditional taxonomic practices—the North American species, instead of being morphologically remote and easily separable from those of South America, show a strong affinity with them (in one case apparently being conspecific), and in general give every evidence of being derived types. The problem, then, is to get certain of the basic forms of the genus out of South America and into North America.

I shall not here enter into controversy with paleobotanists concerning the origins of the floras on the continental masses now called North America and South America, of their relations with the floras of other continental masses, or of the whole problem of paleoclimatology in relation to early plant migrations. "Land bridges" have been invented and later destroyed by contemporary authors; and the whole question of continental displacement in relation to early plant dispersals is in need of clarification, especially when one reviews the more than casual phytogeographic connections of various land masses now widely separated. Considering only the immediate problems of dispersal within the Western Hemisphere, it is becoming evident that once there must have been a much broader land-connection between North America and South America than now exists—a connection which lay to the east of the present narrow "Isthmian Bridge." The sometimes striking phytogeographic affinities between eastern (Atlantic) North America, across the Caribbean and into northeastern and eastern (Atlantic) South America are certainly suggestive of this viewpoint. There is, of course, ample evidence for a series of migrations between the Pacific sides of the two continents.

It would appear that the great bulk of the intercontinental migration

was from the south toward the north.[22] Exceptions are known, but those which I have examined have almost invariably involved the more highly developed and recently evolved members of their group; and, further, these recently arisen members seem, for the most part, to have used the connection on the Pacific side and not spread into South America from North America by an eastward route. Therefore, relying on such phytogeographic and geological evidence as I can gather, I must come to two fundamental conclusions: (1) that a broad land-connection, portions of it probably with considerable altitude, existed for at least part of the Cretaceous between the Atlantic sides of North America and South America, in addition to the generally assumed connection on the Pacific side; (2) that this connection, although broken in the Eocene, was partially reformed at some time during the Oligocene. It is not necessary to assume that, in Oligocene time, the land was completely continuous but, at least for a while, a segment of northern South America must have been connected with an emergent portion of Antillia and this, in turn (perhaps at a later date), with the (then) large offshore island which since has become Florida. The nucleus of this repeatedly expanded and contracted "island" certainly has not been under water since the Eocene and today holds a rich flora derived from the south (being the center, among others, of the distribution of the North American segment of the *Gaylussacia Mosieri-pseudogaultheria* complex). This Florida "island" was connected with the North American mainland during the Miocene.

Returning to our consideration of *Gaylussacia*, it becomes apparent that the genus arose in South America for there, today, we find it as a series of interlocked species-groups still differentiating out of a common plexus, only three of which have given representative members to North America. Nor is it necessary to assume that the early representatives of these groups migrated northward at the same time. Plants very like our modern submontane forms, *G. ursina* and *G. brachycera*, surely must have been in the vanguard of this movement. Here, too, I should like to place the prototype

[22] Any student of the Caribbean floras will immediately recognize that here I am not giving adequate consideration to that region. One of the remarkable things in the Caribbean is its west-east set of phytogeographic connections extending from Central America across the area in such a manner as to make it appear that we are looking at the isolated relics of the floras of an ancient continental mass traversed by a series of nearly parallel mountain ranges. Complicating this picture is the series of well marked south-north lines of connection. The old block of Antillia has been ground between the shifting continental masses of North America and South America; it has been segmented, and the blocks sometimes laterally displaced for many miles; it has been warped and buckled, great folds having been thrown across it in several directions; and it is the directions of the displacements and the trend of these folds and upthrusts—when they were above the waters of those ancient seas—which, to a large extent determined the present complicated floristic pattern of the Caribbean. I am in this place dealing only with a group which apparently crossed from South America *into* North America.

of the wide-ranging *G. baccata* with its upland and lowland forms. *G. tomentosa* and *G. nana*, being somewhat more closely related in habit to species now present in South America, may have arrived later but, even so, they seem to be strongly tinctured with the characters of *G. ursina* and may represent segregate and now nearly homogeneous races following the complete obliteration of a lowland phase of *G. ursina* by several essentially different South American forms.[23] *G. frondosa* gives all evidence of having arisen in North America out of species already present.

There remains for our consideration only *G. Mosieri* and its close relatives. Whether *G. orocola* of the Blue Ridge represents an early introduction into North America and is the form from which *G. dumosa* has been derived, with *G. Mosieri* being a more recent introduction, or whether they all have been derived from the same immediate source, is in the realm of pure speculation and must await further cytological analysis. They are so closely related that I find it difficult to think otherwise than that they have arisen in North America from a common ancestor, in appearance much like the present *G. Mosieri*. Yet, an examination of these and closely related South American forms leads me to the conclusion that *G. orocola* and *G. dumosa* are more nearly related than *G. orocola* and *G. Mosieri;* that the *G. orocola-dumosa* unit came to North America prior to the advent of *G. Mosieri*, but that both of these (the *G. orocola-dumosa* unit and the *G. Mosieri-pseudogaultheria* unit) have been derived from the same South American prototype.

Without correlative data we should be forced to disavow normal peristaltic activity in the avian alimentary tract and call upon our feathered friends for help in some peculiar manner to explain the dispersal of this group of plants over more than short distances. There is, however, another line of evidence which we shall briefly pursue: we shall consider not one species or even a single genus, but a phyletic-ecological consociation. A species of *Gaylussacia* (*G. amazonica* Huber), closely related to the *G. pseudogaultheria-Mosieri* unit and its nearest relatives, is found on the *campos* of the Amazon Basin, a region of comparatively recent origin and historically related to the outer Coastal Plain of North America where various of our own species of this genus are so well developed (at least the regions are both of Late Tertiary and Quaternary age).

[23] I see nothing phyletically improbable in such a viewpoint. It has been accomplished repeatedly in *Vaccinium*, where I have had opportunity to analyze the situation in greater detail against a background of experimental data. In this genus certain species with excellent and "natural" ranges are obviously the result of the blending of heredities of portions of two or more well-marked basic species. In certain instances these "species" (e.g. *V. corymbosum*) have been reproduced by controlled breeding. Furthermore, their characters, consisting of a series of multiple allelemorphs, do not segregate as would be expected of simple unit factors, but enter into combinations forming blended populations in areas of isolation which react much as those of essentially homozygous species. Such, therefore, may easily have been the history of both *G. nana* and *G. tomentosa*.

If we consider even a brief list of the more common plants on these *campos* we will see the close phytogeographic connection between the two areas.[24] To be sure, a group of purely tropical things is present there. But if a student of the flora of the Coastal Plain of eastern and southeastern North America—and one who knows only this flora—were to venture onto those sunny and acid-soil Amazonian savannas he would find many species very similar to those with which he is familiar: examples of *Schizaea*, of Xyridaceae and Eriocaulaceae, *Burmannia*, Melastomaceae, Gentianaceae, various common Gramineae and Cyperaceae, *Cuphea*, *Ilex*, *Brysonima* and *Leucothoë*, to mention only some of those which are more common and which are not widespread "weed-species." Many others could be included.

Perhaps the greatest stumbling block to a complete understanding of the direct south-north migration of *Gaylussacia* is the fact that it is not today known from the interior of the Caribbean area—the region of old Antillia. But its apparent absence is no proof that the genus did not migrate from South America into North America by that route and by gradual steps, without the aid of any spectacular non-stop avian transportations. The exact sequence of geological events throughout the Caribbean is still much in question and one needs only refer to the work of Hess on the basic island arc structure in the West Indies[25] to sense the variant opinions and the need for a reinterpretation of the geohistory of this region. This is particularly true of those areas which, periodically or locally for long periods, have been out of water and colonizable by plants, rather than those which have been so often inundated. It is obvious that whole segments of Antillia have been lost, some of these apparently rather late in the Tertiary; segments which, if they were above water today, might serve to clarify what, to us, seems to be a rather complicated and insoluble sequence of plant migrations, often not at all correlated with the present series of "island stepping stones" which swing the arc of the Caribbean (see again footnote 22).

I have little hope that *Gaylussacia* will yet be found even in the poorly explored and geologically ancient mountainous parts of Oriente in Cuba or on the pre-Tertiary Cordillere Centrale of Hispaniola, but the possibility should not be excluded. Such a discovery would certainly be welcome news to an ericologist. However, it is more likely that such members of *Gaylussacia* as might have been on Antillia during the Tertiary were, like most of their congeners, poorly adapted to compete under tropical forest conditions and must have existed only in sunny, acid savannas, or at most associated with open forest stands, even as today.

[24] Ducke, Adolph. A Amazonia Brasileira. Anais Prim. Reun. Sul-Amer. Bot. **1**: 275–287. 1938. For a discussion of these Amazonian *campos* and the related and widespread non-forested areas to the southeast, the center of *Gaylussacia*-concentration in Brazil, see: de Sampio, A. J. Phytogeographia do Brasil. Bol. Mus. Nacional (Rio de Janeiro) **6**: 271–299. 1930; especially the map opp. p. 296.

[25] Hess, H. H. Proc. Am. Phil. Soc. **79**: 71–96. 1938.

If I am interpreting the available evidence correctly it would appear that the Oligocene was the last chance for the *Gaylussacia*-population of South America to place members within easy striking distance of North America by natural means of dispersal and, if we *must* call in the birds, without forcing them to fly unreasonable distances over water. This is brought out particularly well by one of Schuchert's maps (*l.c.*, Plate 11). I would, for the present, want to make only one important change in this chart. It is my opinion that, during the Lower Oligocene at least, the eastern part of Antillia was connected with parts of northern South America by a broad band of open, mixed lowland-savanna country; a type of terrain which must have extended northward in broad arcs to the margin of present-day Florida, being then separated from the Florida "island" by only a narrow strait, probably less than 100 miles wide, and easily crossed by birds. Or it is possible that these areas may even have had actual surface communication for a time and that more recent geological events have obscured the record.

The Miocene witnessed the extreme deformation and almost complete submergence of the bulk of Antillia, leaving emergent only a few small and widely separated islands. There was a brief recovery during the Lower Pliocene, but the Pleistocene again brought on a rather general inundation; this being followed by a recent partial uplift.

Had such members of *Gaylussacia* as were on central and eastern Antillia in the Oligocene been so placed that they could migrate into these small residual island centers of refuge during the Miocene and Pleistocene submergences, it is unlikely that they could have competed with the forest vegetation already there. Of it they could have, the recovery (as in Cuba) of available and ecologically suitable habitats at the end of the Pleistocene would have been most difficult, for large areas were now highly charged with marine calcareous salts, always fatal to a group—such as *Gaylussacia*—which requires acid-soil conditions.

Briefly then, beginning in the Late Tertiary, the history of Antillia was such that it practically excluded any possibility of *Gaylussacia* having remained there; whereas conditions during part of the Cretaceous and again during the Oligocene would seem to have been ideal for trans-Antillian plant migrations.

We can, I think, exclude any possibility of the genus having come into North America by way of Central America and Mexico, in part the western segment of Antillia. There are today in those regions too many groups of the Ericales having a strong relationship (even conspecific) with those of eastern North America and which (in the latter) have the same ecological requirements as *Gaylussacia*. Had the genus come by that route in sufficient numbers so as to have given the morphologically different and ecologically

distinct forms which now exist in North America, some would surely have been preserved along with their ericalean relatives. But none are known.

*Conclusions on the migrations into North America.* It is on the foregoing set of collateral evidences that I base my first conclusion that there probably were two major cycles of immigration of the genus *Gaylussacia* into North America. Although having today an obvious phyletic connection with forms now existing in South America, the upland and apparently earliest of these immigrants seem to have had sufficient time to evolve into species quite distinct from their nearest relatives. The more recent introductions into North America appear to have been mainly lowland forms and show no such marked differences being, in part, apparently conspecific with South American material. It is also concluded that the propagules of the ancestral forms giving rise to the present species were not carried directly from South America into North America, but that the dispersal was of a type normal to the group—one by gradual migration on land then existent, or at most for only short distances across water. Lastly, it is concluded that the migration was across the eastern portion of Antillia and not by the present "Isthmian Bridge."

## SUMMARY

An examination of the Gaylussacieae, a tribe of the Vacciniaceae, reveals that, as a group, it has undergone its major evolution in South America. There, definite lines of phyletic divergence are evident, but it is obvious that they have been derived out of a common plexus, forms being present today which bridge the gap between the more primitive members of these groups. As a consequence, it would seem prudent not to attempt any generic segregation within the South American representatives; that they all be considered as part of the genus *Gaylussacia*.

It has been traditional for the past century to consider the North American Gaylussacieae as being in some way easily separable from the South American forms, for they have been treated by various authors as separate sections of a genus, as subgenera, or even different genera. Considered alone, the North American material consists of three well-marked groups, but when critically examined each of these gives clear indication that it has been rather directly derived from South American material, having counterparts in the common plexus of the genus. In one instance there is even an apparent specific link between the two continents. If the South American material is to be maintained as a single genus, it is therefore obvious that the North American forms must be included. It is certainly clear that any separation into subgeneric categories on a geographic basis violates the fundamental phylogeny of the group.

It is evident that the genus *Gaylussacia* has undergone its major develop-

ment on the ancient uplands of southeastern Brazil; that some of its lines of descent are also represented in northern and northwestern South America; and that derived but closely related forms are present in North America. From this evidence we must conclude that the genus migrated into North America from South America.

It seems apparent that there were two major introductions of the genus *Gaylussacia* into North America; one, primarily of upland forms, during the Cretaceous and another, of lowland forms, during probably the Oligocene.

Since there is no evidence that the genus entered North America by way of the present "Isthmian Bridge," or even in the same region by a much earlier connection, it is concluded that the northward migration of *Gaylussacia* must have taken place across the eastern segment of Antillia. This opinion is further substantiated, not only by certain present close relationships within the genus but also by residual, but strong, phytogeographic connections in other groups between parts of eastern South America and eastern North America. The absence of the genus today from the interior of the Caribbean area is no proof that the group did not move northward by that route, for the Late Tertiary and Recent history of the area involved a series of events resulting in the formation of habitats ecologically unsuited to its survival there.

*Gaylussacia*, an obviously ancient genus is, therefore, another of those genetic complexes giving clear indication of the derived nature of the North American floras. It is another link in the ever strengthening chain of evidence that many angiospermous groups underwent their primary evolution in the Southern Hemisphere and subsequently migrated into the Northern Hemisphere.

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# SUPPLEMENTARY NOTES ON AMERICAN LABIATAE—II[1]

CARL EPLING

TEUCRIUM

T. BICOLOR Sm. CHILE—COQUIMBO: Depto. Ovalle, Cuesta de Cavilolin, *Worth and Morrison 16453.* Depto. Illapel, Quebrada Luncuman, *Worth and Morrison 16502.* SANTIAGO: Depto. Melipilla, La Viscachas, associated with *Schizanthus, Phacelia* and *Alstroemeria spathulata.* The flower color of this species, as with the following, may vary from pure white or cream-color to maroon, at least on the lower lip. Both extremes grow together.

T. NUDICAULE Hook. CHILE—ATACAMA: Depto. Huasco, near Huasco, *Worth and Morrison 16428.* "Flower cream-colored; lip white-pubescent, velvety maroon inside. Two collections of apparently this same genus at Taltal (viz. *Worth and Morrison 15832; Beetle 26177*) but none with this color lip. Some here lacked it" (collectors' note). Depto. Elqui, 20 km. al sur de Vicuña, *Wagenknecht 4237.*

T. LAEVIGATUM Vahl. ARGENTINA—BUENOS AIRES: 77 km. southeast of La Plata near mouth of Rio de la Plata, *Eyerdam and Beetle 23275.*

STACHYS

S. LINDENII Benth. GUATEMALA—SAN MARCOS: Volcan Tacana, 2500–3000 m., *Steyermark 36264.* SUCHITEPEQUEZ: Volcan Zunil, 500–800 m., *Steyermark 35439.*

S. ERIANTHA Benth. MEXICO—VERA CRUZ: Los Pescados, 10,500 ft., *Balls 4607;* Apitza, Ixtaccihuatl, 12,600 ft., *Balls 5137.*

S. (?) GLOBOSA Epling. MEXICO—VERA CRUZ: Loma Grande, Mt. Orizaba, 9,200 ft., *Balls 4353.* Assuredly a member of the species group to which *S. globosa* is assigned, characterized by the relatively short upper lip and scarcely exserted stamens. However, although the pubescence is very like that of *S. globosa,* the flowers are larger and the calyx teeth less pronouncedly spinose.

S. TRUNCATA Kunze. CHILE—ANTOFAGASTA: Depto. Taltal, 6 km. east of Taltal, *Worth and Morrison 16117.* Assuredly this species, previously known no further north than Coquimbo, and with a slight but unmistakable annulus in the corolla tube.

S. BORAGINOIDES C. & S. MEXICO—MICHOACAN: Mt. Tancitaro, near Uruapan, 2075 m., *Hinton 15501.* Apparently referable to this species, previously known only from Vera Cruz and Hidalgo.

S. APERTA Epling. This species is known only from a single specimen collected by *Macbride* near Muna (*no. 3963*). The present specimen, collected by *Worth and Morrison* (*no. 15661*) in PERU, Depto. AREQUIPA, Prov. Camana near Atiquipa, corresponds fairly well, save in the degree of exsertion of the stamens. In the type, they are exserted 3 mm.; in this specimen, about 1.5 mm. To this specimen may also be added one collected by *Killip*

[1] See Bull. Torrey Club 67: 509–534. 1940.

*and Smith* (*no. 22253*) in Depto. AYACUCHO at Pampalca, between Huanta and Rio Apurimac and one collected in Arequipa near Chala by *Weberbauer* (*no. 7191*). Whether these are conspecific remains to be determined by more collections. Suffice it to say that they are the only known Peruvian *Stachys* of this habit, with corolla tubes 6–8 mm. long, which have a well-defined annulus. They are apparently the Peruvian representatives of a complex group which ranges from Chile (*S. Macraei*) to California (*S. bullata*).

SCUTELLARIA

S. (?) HOOKERI Epling. COLOMBIA—Comisaria del CAQUETÁ, Cord. Oriental, Quebrada del Rio Hacha, Cajon de Pulido, 1700 m., *Cuatrecasas 8747* (Herb. Nac. Colomb.). This species was described from cultivated plants, grown from Peruvian seeds. *Poeppig 1535*, collected near Pampanacio, Peru, is seemingly identical with the type. The present specimen is identical in pubescence with Poeppig's plant, pubescence unique in the South American species of *Scutellaria*, and is very similar in habit. The leaves of Poeppig's plant are pale and seemingly whitish beneath, whereas those of the present specimen are purple beneath.

S. BENTHAMIANA (Mansf.) Epling. PERU—APURIMAC: Prov. Abancay, slopes of Orckone Grande, Trancapata, near Curasuasi, 3100 m., *Vargas 9622*. Said by the collector to have been collected by him also in Paruco, Cuzco.

HEDEOMA

H. FLORIBUNDUM Standley. MEXICO—SONORA: Sierra des Pappas, *Gentry 631*.

MINTHOSTACHYS

M. MOLLIS Griseb. PERU—LA LIBERTAD: Prov. Santiago de Chuco, north of Cachicadan, *Stork and Horton 9957*.

SATUREJA

S. TAXIFOLIA (Kunth) Briq. ECUADOR: Cuenca, Quebrada de Chushkin 8,500 ft., *Balls 7079*.

S. ACUTIFOLIA (Benth.) Briq. PERU—CAJAMARCA: Prov. Cutervo, Sucse R. Valley west of Socota, 2800 m., *Stork and Horton 10097*. Known previously only from the original collections of Mathews at Chachapoyas. Those specimens are notably silky with appressed hairs on the upper leaf surface and twigs. The present specimens are hardly silky in pubescence, but have the same habit and essentially the same flowers. The calyx teeth, however, are as much as 4 mm. long.

**S. Panicera** Epling, sp. nov. (Gardoquia). Frutex altitudine ad 1.5 m. ramulis pilis brevibus subappressis hirtellis; foliorum laminis crassiusculis obtusis modo rhomboideis et in basi cuneatis modo deltoideo-ovatis et in basi truncato-subcordatis, 1–2.5 cm. diametro, marginibus serrato-crenatis, revolutis, pagina superiore rugosa glabra viride, inferiore dense albo-tomentosa; petiolis 2–5 mm. longis; floribus circiter 6 in cymulis breviter pedunculatis axillaribus, bracteolis linearibus 3–4 mm. longis subtentis; calycibus costatis extus pilis brevibus crispule hirtellis, tubo circiter 6 mm. longo et dentibus deltoideo-lanceolatis acutis, inferioribus 3.5–4 mm. longis, superioribus

similibus in basi connatis; corollarum auriantiacarum tubo 20–25 mm. longo, labia superiore 4–5 mm. alta.

PERU—LA LIBERTAD: Prov. Santiago de Chuco, Cachicadan, 2800 m., *Stork and Horton 9956* (TYPE, Univ. Calif., L. A.).

In habit this proposed species is scarcely different from *S. rugosa* (R. & P.) Briq. and very similar to *S. tomentosa* (Kunth) Briq. The first named is known only from the type, the locality of collection of which is not known, save that it is ascribed to Peru. The second named is an Ecuadoran species, frequently collected. It is known from Peru from a single collection made near Huanta by *McBride and Featherstone (no. 2084)*; it is not certain, however, that this specimen is conspecific with the plants of Ecuador. The flowers are similar. The present specimen differs from both *S. rugosa* and *S. tomentosa* primarily in the flowers. The calyces of *S. rugosa* are about 7 mm. long, with a fine spreading pubescence, the teeth being about 2.5 mm. long. The corollas are notably shorter, the tube being only about 1 cm. long. While it is true that the corollas of *S. tomentosa* are about the same as those of the present plant, the calyx teeth appear to be uniformly shorter, rarely over 2.5 mm. long. Much more material is needed satisfactorily to dispose of this complex.

According to the collector's note the species is gathered in the locality cited and sent to Trujillo for sale in the market as a medicinal herb. It is known as "Panicera."

ASTEROHYPTIS

A. SEEMANNII (Gray) Epling. MEXICO—DURANGO: Tamazula, *Gentry 5224*.

HYPTIS

H. (?) SIDAEFOLIA (L'Hérit.) Briq. Inadequate collections of what are probably this species have been collected in PERU—ANCASH: Prov. Santa, Lomas de la Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9203*. AREQUIPA: Prov. Camana, 10 km. east of Chala, *Worth and Morrison 15618*.

H. INVOLUCRATA Benth. MEXICO: Temascaltepec, Penon, 1700 m., *Hinton 2146;* Temascaltepec, Tejupilco, *Hinton 1597*. Previously known only from Bentham's type, collected at Saltepec by *Karwinski*. Both specimens, like the type, have the leaves and capitula in threes. The involucre is very conspicuous.

H. HIRSUTA Kunth. A specimen which is apparently referable to *H. hirsuta* Kunth, has been collected in Los Llanos, Rio Meta, near Matabubosa by *Cuatrecasas (no. 4242)*. If this species, it is the first time it has been found in Colombia, although known from Venezuela. However, the columella of the gynobase, which in *H. hirsuta* equals the ovules in length, is seemingly wanting in this specimen. The nutlets are alveolate, however, a characteristic of the section *Xylodontes* to which *H. hirsuta* is assigned.

**H. villicaulis** Epling, sp. nov. (*Polydesmia: Vulgares*). Herbae perennes utrimque pilis longioribus molliter pilosae; foliorum laminis sat amplis, 8–11 cm. longis, late rhomboideo-ovatis, 6–9 cm. latis, in apice leniter acuminatis, in basi plus minusve cuneatis, marginibus dupliciter serratis, paginis ambabus molliter pilosis; petiolis plus minusve marginatis, 1–3 cm.

longis; verticillastris in spicis compactis, pedunculis circiter 2 mm. longis elatis; bracteis paucis, vix membranaceis, circiter 5 mm. longis acuminatis mucronatis, ciliatis et paulo villosis, calycibus florentibus circiter 3 mm. longis, dentibus tubum subaequantibus, setaceis, vix tamen rigidis, equilongis, tubis maturis 5 mm. longis, tenuibus, dentibus fere 2 mm. longis; corollarum tubis 5 mm. longis; nuculis oblongis in apice rotundatis.

BRAZIL—MATTO GROSSO: Maribondo, Rio S. Lourenco, IV. 1911, *Hoehne 2866* (TYPE, Univ. Calif., L. A.).

**H. brachypoda** Epling, sp. nov. (*Cephalohyptis: Marrubiastrae*). Herbae versimiliter perennes caulibus utrimque pilis ascendenti-appressis molliter hirsutis, internodiis superioribus quam folia fere duplo longioribus; foliorum laminis subcoriaceis, ovatis, 6–7 cm. longis, circiter 3 cm. latis, in basi rotundato-angustatis, supra medium acuminatis, marginibus sat convexis, regulariter serratis, pagina superiore sparse appresso-hirsuta, tamen sublucida, inferiore pallidiore praesertim ad venas appresso-hirsuta plus minusve sericea; petiolis latioribus subnullis 5–8 mm. longis; capitulis maturis globosis circiter 1.5 cm. diametro, in foliorum superiorum vix deminutorum axillis pedunculis hirsutis 3–3.5 cm. longis elatis; bracteis lanceolatis 7–9 mm. longis, mox reflexis, hirtellis; calycibus florentibus 4 mm. longis, dentibus deltoideo-subulatis fere 2.5 mm. longis, fere glabris, tubo in maturitate 4 mm. longo, glabro; corollarum tubo 3.5 mm. longo; nuculis obscure asperulis ut videtur laevibus.

COLOMBIA—ANTIOQUIA: Cocorua, VIII. 1938, *Bro. Daniel 1530* (USNH, type). In habit this plant suggests *H. brachiata* (*Xylodontes*), also Colombian. However, the structure of the gynobase and the obscurely roughened rather than alveolate nutlets, relate it to *Cephalohyptis*.

**H. pseudolantana** Epling, sp. nov. (*Rhytidea*). Frutex vel suffrutex altitudine circiter 1 m., superne sat sarmentosus, nullomodo virgatus, ramulis pilis crassiusculis in basi plus minusve pustulatis ascendentibus scabropubescentibus et superne glanduloso-puberuliis; internodiis foliorum laminas subaequantibus; foliorum laminis ovatis, vix membranaceis, 1.5–2.5 cm. longis, in apice sat acutis, in basi rotundatis, paginis ambabus scabro-hirsutis, marginibus leniter et irregulariter serratis; petiolis 1–2 mm. longis; cymulis axillaribus pedunculis 3–5 mm. longis elatis; calycibus florentibus 4.5–5 mm. longis, extus dense glanduloso-puberulis et sparse ciliatis, intus supra medium piloso-annulatis tubis dentes subaequantibus sat tenuibus, dentibus deltoideo-lanceolatis, acutis; calycibus maturis etiam nuculis non visis; corallarum tubis 5.5–6.5 mm. longis.

The habit, not unusual for *Hyptis*, strongly suggests some species of *Lantana*, such for example, as *L. montevidensis*. The structure of the calyx, with its median annulus, suggests its association with *H. rhytidea*.

MEXICO—GUERRERO: Aguazarca Filo, distr. Mina, *Hinton 11266* (TYPE, Univ. Calif., L. A.).

**H. pseudosinuata** Epling, sp. nov. (*Cephalohyptis: Marrubiastrae*). Herbae verisimiliter perennes caulibus superne tenuiter villosis, internodiis quam folia longioribus; foliorum laminis ovatis, 4.5–5 cm. longis, 2.5–3 cm. latis (et grandioribus in partibus inferioribus?), obtusiusculis, in basi rotundatis et ad petiolos 5–15 mm. longos plus minusve cuneatis, marginibus regulariter serratis, paginis ambabus fere glabris, tenuiter villosis; capitulis

maturis subglobosis, 18–22 mm. diametro, viridibus, in foliorum supremorum gradatim deminutorum axillis pedunculis 10–12 mm. longis dispositis; bracteis villosis, anguste ovatis, 5–6 mm. longis, in maturitate occultis; calycibus florentibus fere glabris, circiter 3.5 mm. longis, dentibus circiter 1.5 mm. longis, anguste deltoideis, acutis, subaequalibus, tubo in maturitate 3.5 mm. longo; corollarum tubo 3.5 mm. longo.

COLOMBIA—HUILA: Cordillera Oriental, bosques mas arriba de Guadalupe en Resina, 1850–1900 m., 20.III.1940, *Arbolaez and Cuatrecasas 8363* (USNH, TYPE).

SALVIA[2]

Key to Sections (p. 7, line 36). Read for "Invaginatas" "Hoehneana et."

5. S. SETOSA Fern. MEXICO—DURANGO: Tamazula, *Gentry 5243.* Apparently this, but the corolla tubes 4 mm. long and the lips proportionately longer, but still hardly equal to those of *S. monantha.*

41. S. LAVANDULOIDES Kunth. MEXICO—DURANGO: Sierra Tres Picos, *Gentry 5332.* SONORA: La Mesa Colorado, *Gentry 546.* SINALOA: Cerro de la Sandia near Panuco, *Pennell 20106.* Previously known no further north than Jalisco. These specimens seem fairly typical and are comparable to Guatemalan specimens, as for example, *Standley 58580.* The Sonoran specimen is more glabrate, but scarcely to be distinguished from *Hinton 134,* from Temascaltepec. GUATEMALA—ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29701.* SAN MARCOS: Sibinal, 2500 m., *Steyermark 36070.* JALAPA: Cerro Alcoba, near Jalapa, 1300–1700 m., *Steyermark 32604;* between Quisiltepeque and Potrero Carrillo, 1800 m., *Steyermark 33020;* same place, *Steyermark 33021* (an albino).

47. S. ALAMOSANA Rose. MEXICO—SINALOA: Cerro Colorado, *Gentry 5210.* SONORA: Saucito canyon, distr. Alamos, *Gentry 688.* The second specimen, from the type locality, has sparse spreading glandular hairs in the inflorescence instead of the usual downwardly curled ones.

50. S. INCONSPICUA Benth. MEXICO—MICHOACAN: Sierra Torricillas, Coalcoman, 2420 m., *Hinton 12402; 12361.* GUERRERO: Toro Muerto, Mina, 2350 m., *Hinton 14763;* Teotepec, distr. Mina, 2500 m., *Hinton 14806.*

52. S. CHALAROTHYRSA Fern. MEXICO—MICHOACAN: Coalcoman, 1200 m., *Hinton 12329;* Coalcoman, Salitre, 1200 m., *Hinton 12171.* Known previously only from the type, collected in Jalisco.

54. S. PAVONII Benth. PERU—JUNIN: Prov. Tarma, between Palca and Carpapata, 2900 m., *Stork 10956.* Previously known only from the type, collected in Peru without data by (?) Dombey. The leaves of this specimen are somewhat more lax than the type, now at the University of Oxford, otherwise it is very similar. The sessile glands which cover the leaves and branches are evidently quite conspicuous and are said by Stork to be cinnabar red. The corollas are lemon yellow. What appears to be the same species was collected, supposedly by *Lobb* (*no. 82*), and attributed to Colombia by Hooker.

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[2] The serial numbers and cited paginations refer to a previous paper, "Revision of Salvia: Calosphace" in Rep. Spec. Nov., Beih. 110. 1939.

57. S. CORRUGATA Vahl. PERU—HUANCAVELICA: Prov. Tayacaja, Quebrada south of Salcabamba, 3300 m., *Stork and Horton 10297*. The flowering calyces are 9 mm. long and the corolla tubes are 18 mm. long, the upper lip being 10 mm. long.

58a. **S. pseudorosmarinus** Epling, sp. nov. (*Corrugatae*). Suffrutex altitudine ad 60 cm. ramis virgatis viscidis pilis minutis extensis glandulosis et majoribus crispis eglandulosis vestitis superne villosis, utrimque ad basim ramulis brevibus foliis fastigiatis ornatis submoniliformibus; foliorum laminis bullulatis habitus *Rosmarini* linearibus 1–2.5 cm. longis, valde revolutis, in apice obtusis, in basi modo truncatis modo hastatis, pagina superiore minute glandulosa inferiore obumbrata villosa; petiolis 1–3 mm. longis; floribus ut videtur solitariis in foliorum supremorum paulo deminutorum axillis positis; calycibus florentibus 9–10 mm. longis, extus viscido-villosis, trimucronatis; corollarum atro-cyanearum tubo 15 mm. longo, labia superiore 5 mm. alta, inferiore fere duplo longiore.

PERU—LA LIBERTAD: Prov. Santiago de Chuco, Cachicadan. Open shrubby hillside, clay soil, 2900 m., 25.XI.1938, *Stork and Horton 9968* (TYPE, Univ. Calif., L. A.).

This species bears all the earmarks of the section *Corrugatae* save for the fact that the flowers are borne in the axils of the upper but little modified leaves. It would accordingly be sought under *Tomentellae* in the Key to the Sections (p. 9). The Key should therefore be emended to read (p. 9, line 28) as follows:

"HH. Frutices sarmentosi vel suffrutices pilis frequenter ramosis; styli ramus anticus sat attentuatus vix complanato-deltoideus. I. Corollarum tubi ad basim valde invaginati; folia habitus *Rosmarini* 11. *Corrugatae*. II. Corollarum tubi sat ventricosi, vix tamen invaginati nisi rugis binis obliquo intus obscure ornati 3. *Tomentellae*. DD. Staminum gubernacula vel integra, etc., etc."

The foliage and the dwarf lateral branches are highly distinctive and closely simulate those of Rosemary.

99a. S. RHOMBIFOLIA R. & P. PERU—ANCASH: Prov. Santa, Lomas de Mongon near San Rafael, between Casma and Huarmei, *Stork, Horton and Vargas 9177*; same, Lomas de La Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9213*.

110. S. SAGITTATA R. & P. PERU—LA LIBERTAD: Prov. Santiago de Chuco, above Cachicadan, 2800 m., *Stork and Horton 9958*.

111. S. RHODOSTEPHANA Epling. PERU—AYACUCHO: Ocros, Pajonal to Ayacucho, 9000 ft., *Balls 6925*. A more accurate description of the corolla is now possible. The tubes vary from 22–25 mm., the upper lip from 7–9 mm., the lower lip being about twice as long. The stamen connective is 30–40 mm. long. The color may vary from pink to "blue or pale mauve."

118. S. MENDAX Epling. GUATEMALA—JALAPA: Between Quisiltepeque and Potrero Carillo, 1800 m., *Steyermark 33073*. ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29739*.

### *21A. Gentryana*

Herbae perennis sat crassae pilis ramosis molliter pubescentes foliis sat magnis ovatis petiolatis; floribus pedicellatis, tribus in verticillastris bracteis

parvis caducis subtentis in spicas axillares vel spremas paniculatas confertis; calycum parvorum truncatorum labia superiore 5-venis; corollarum roseo-purpurearum tubo recto intus nudo quam calyces duplo longiore, labia superiore erecta vix galeata, inferiore latiore vix tamen quam superior longiore; staminibus ad fauces positis ultra labiam superiorem exsertis, gubernacula integro vel ad connexum dente extenso ornato; styli glabri ramo postice subnullo.

122b. **S. trichostephana** Epling, sp. nov. (*Gentryana*). Herba perennis crassa altitudine ad 2 m., ramis pilis ramosis sat dense vestitis internodiis speciminis suppetentis quam folia brevioribus; foliorum laminis ovatis, 8–11 cm. longis, 4–7 cm. latis, crenato-serratis, pagina superiore pilis ramosis parvis sparse conspersa, inferiore cinerea; petiolis 2–2.5 cm. longis; spicis gracilibus sat confertis 5–6 cm. longis, inferioribus axillaribus, superioribus paniculatis; floribus tribus in verticillastris bracteis caducis parvis subtentis, pedicellis 3 mm. longis elatis; calycibus florentibus 2.5 mm. longis, subtruncatis, pilis simplicibus subappressis hirtellis in maturitate non visis; corollarum roseo-purpurearum tubo 5 mm. longo, recto, labia superiore 2.5 mm. alta, inferiore aequilonga rotunda; staminibus ultra labiam superiorem 3 mm. exsertis; gynobasis cornu quam nuculae triplo longiore.

MEXICO—SINALOA: Puerto a Tamiapa, 6–8.III.1940, *Gentry 5846* (TYPE, Univ. Calif., L. A.).

This remarkable plant does not resemble any other continental section in floral structure, but suggests most nearly the section *Wrightiana* of Cuba and Haiti. That section differs however in the fact that the upper lip of the calyx is 3-veined, the lower lip of the corolla is longer than the upper, the corolla is blue and the pubescence simple.

In the Key to the Sections (p. 6, line 34) this section would be sought near *Hastatae*, *Micranthae* and *Rhombifoliae*. That portion of the Key should therefore be emended to read as follows:

"CC. Calycum labia superior 5–7 venis et ultra. D. Corollarum tubi 3.5–6 mm. longi; styli glabri ramus posticus saepius brevior etiam subnulli. E. Folia palaeforma; flores oppositi caerulei; herbae procumbentes colombianae (vide etiam *Blakea*) 18. *Hastatae*. EE. Folia ovata vel deltoideo-ovata; flores 2–6 in verticillastris et ultra. F. Herbae perennes sinaloenses crassae ramis pilis ramosis vestitis; corollae roseo-purpureae 21a. *Gentryana*. FF. Herbae parvae saepius annuae pilis simplicibus vesitae; corollae caeruleae. G. Stamina e labia superiore vix exserta; plantae borealiamericanae nisi insularum Galapagos 14. *Micranthae*. GG. Stamina sat exserta; plantae andinae 16. *Rhombifoliae*. DD. Corollarum tubi 10–43 mm. longi, etc., etc."

134. S. HIRTELLA Vahl. ECUADOR—TUNGURAGUA: Mocha, Hacienda Yanagaca, 10,000 ft., 7.XI.1939, *Balls 7184*. "Leaves small, making a dense mat several feet across, on stems which creep along the ground and from which the flower stems stand upright." The bracts may be deciduous in fruit.

135a. (149) S. PRAECLARA Epling, Rep. Spec. Nov., Beih. **85**: 121. 1936. A shrub or perennial herb as much as 2 m. tall, its stems glandular and viscid with spreading hairs of varied length, as much as 2 mm. long; leaf blades membranous, commonly 6–12 cm. long, 5–12 cm. broad, mostly deltoid in outline, somewhat acuminate at the apex, broadly and definitely

cordate at the base, or the upper ones deltoid-lanceolate and subtruncate, their margins irregularly and rather coarsely crenate or serrate, both surfaces bright green and nearly glabrous, thinly glandular on the upper surfaces with spreading hairs, and along the veins beneath; bracts fugacious, 3–5 mm. long, ovate-acuminate, hispidulous; flowers several in each verticil, the glomerules at length 1–3 cm. distant; flowering calyces 8–11 mm. long, often reddish toward the tips, glandular with spreading hairs similar to those of the stems, 12–13 mm. long at maturity, the lower calyx teeth partially connate, the mature pedicels 5–6 mm. long; corolla bright clear crimson, its tube 14–25 mm. long, bearing an elliptical dense areole of stiffish short hairs on the lower side above the ovary, the upper lip 7–8 mm. tall, the lower about twice as long, the middle lobe ample; stamens seated about 3 mm. below the orifice, the filaments 7–9 mm. long, the connective 30–32 mm. long, the rudder 12–13 mm. long, bearing a sharp spreading tooth 1.5 mm. long, which projects from the throat.

Previously known only from the type, collected by Pearce in Mecoya Valley. The following specimens have permitted a more accurate description of this species and, with adequate material of the corollas, its assignment to Sect. *Mineatae* rather than Sect. *Cylindriflorae*. This species not improbably has horticultural value. According to Eyerdam it is sweetly scented with the odor of lemon.

BOLIVIA—COCHABAMBA: Prov. Mizque. Vilavila, 2500–2600 m., *Eyerdam 25079, 25022, 25329;* 3 km. south of Cochabamba, 2800 m., *Eyerdam 24929, 24931;* 1 km. northwest of Vilavila, 2500 m., *Eyerdam 24974.*

The Key to the Sections (p. 7, line 11) should be amended to read as follows:

H. Plantae Argentinae et Bolivianae; bracteae deciduae ..... 28. *Mineatae.*

The Key to section Mineatae should read as follows:

Calyces florentes 14–17 mm. longi; corollarum tubi 23–28 mm. longi; plantae argentinae ..... 135. *S. exserta.*
Calyces florentes 8–11 mm. longi; corollarum tubi 14–25 mm. longi; plantae bolivianae ..... 135a. *S. praeclara.*

141. S. TUBIFLORA Sm. PERU—ANCASH: Prov. Santa, Lomas de La Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9202.*

142. S. STRIATA Benth. PERU—APURIMAC: Prov. Andahuaylas, Pincos, 2700 m., *Stork and Horton 10667.* "In fields everywhere; an annual herb to .5 m.; common eastward as far as Cuzco."

143. S. OPPOSITIFLORA R. & P. PERU—CAJAMARCA: Prov. Hualgayoc near Bambamarca, *Stork and Horton 10030.* The pubescence of the inflorescence and calyces is quite variable in this and in a second collection from Depto. Lima. The calyces and branchlets may be either glabrate, with a few eglandular hairs, or spreading-glandular.

154. S. HAENKEI Benth. BOLIVIA—CHUQUISACA: Near Sucre, 8,500 ft., *Balls 6174.*

173. S. CINNABARINA M. & G. GUATEMALA—JALAPA: Volcan Jumay, 1800–2200 m., *Steyermark 32433;* Cerro Alcoba, near Jalapa, 1300–2200 m., *Steyermark 32538.*

177. S. ORBIGNAEI Benth. BOLIVIA—CHUQUISCA: Near Sucre, 8,500 ft., *Balls 6151.*

184. S. NITIDA (Mart.) Benth. MEXICO—GUERRERO: Sierrita near Galeana, 950 m., *Hinton 14997.* Known previously only from the type, collected at Juquila in Oaxaca.

189. S. MOCINOI Benth. GUATEMALA—SAN MARCOS: Volcan Tajumulco, 1300–1500 m., *Steyermark 37959.* The lips of the calyx tube of this specimen are scarcely 1 mm. long.

202a. **S. trifilis** Epling, sp. nov. (*Flocculosae*). Herba perennis caulibus ascendentibus altitudine ad (?) 60 cm., inter folia pilis extensis simplicibus eglandulosis sparse ornatis, inter flores extensis glandulosis dense vestitis; foliorum laminis ovatis 3–5 cm. longis, 2–3.5 cm. latis, in apice acutiusculis, in basi rotundatis (? interdum subcordatis), marginibus serrulatis, pagina superiore viride pilis simplicibus interdum ramosis sparse hirsuta, inferiore cinerea pilis ramosis sat tomentosa; petiolis 1–2.5 cm. longis elatis; floribus circiter 6 in verticillastris bracteis caducis subtentis, glomerulis caeruleis inter se 1–2.5 cm. distantibus in spicis interruptis 15–20 cm. longis dispositis; calycibus florentibus 6 mm. longis extus pilis extensis glandulosis ut videtur viscidis, labiis sat hiantibus acutis in maturitate paulo auctis; corollarum caerulearum tubo 6.5 mm. longo, labia superiore 3.5 mm. alta.

PERU—CAJAMARCA: Prov. Cuteros, Suese River Valley west of Socota, 2800 m., *Stork and Horton 10105* (Univ. Calif., L. A., TYPE).

This species might readily be mistaken for *S. cuspidata,* known from Lima. However, the stamen structure and the branched pubescence of the leaves readily distinguish it. In habit and pubescence it also resembles some of the species of *Scorodonia,* a Mexican section, such for example as *S. melissodora.* However, the herbaceous rather than fruticose habit, the more spreading jaws of the calyces and the epapillate corolla tubes distinguish it from that group.

224a. S. CAPILLOSA Epling. A reconsideration of this species, together with *S. sapinea,* suggests the essential unity of the sections *Scorodonia* and *Urica,* although the extremes are rather diverse. Until more material is available for better understanding of the complex, it seems preferable to consider them as a single section, which would preferably take the name of *Scorodonia.* The Key to the Sections which refers to them can be bettered to read as follows (p. 11, line 37):

"KK. Corollae saepius caeruleae vel cyaneae, rarius albidae vel roseo-purpureae; caules vix decurrenti-villosi; plantae imprimis mexicanae. L. Corollarum caerulearum vel albidarum labia inferior quam galea longior (vide etiam 59a *Nivalis;* corollae albae albo-pilosae). M. Folia modo oblongo-lanceolata vel linearia et bractea saepius decidua modo ovata tamen bractea saepius perstata; corollarum tubi intus nudi (*S. leptophylla* et *similis* exceptae) 46. *Farinaceae.* MM. Folia ovata vel deltoidea (*S. occiduae* oblongo-lanceolata); bractea decidua; corollarum tubi intus ad basim rugis binis vel papillis ornati, rarius nudi 43. *Scorodonia.* LL. Corollarum cyanearum vel roseo-purpurearum labia inferior quam galea subaequilonga vel brevior. M. Folia deltoidea, bullulata; corollarum tubi albi, labiae cyaneae 52. *Atratae.* MM. Folia ovata-elliptica in basi angustata (*S. festivae* rotundata); corollae vix bicolores. 59. *Maxonia.*"

Following is a suggested modification of the Key to *Scorodonia* to include the species of *Uricae* (p. 167, line 18 seq.):

Corollarum tubi 5–15 mm. longi; folia pilis longioribus saepius appressis frequenter glandulosis hirsuta, interdum glabra.
Folia plerumque 4 cm. longa et ultra; petiolis saepius plus quam 1 cm.; ramulorum pili magnam partem 2–3 mm. longi.
Corollarum tubi 5–7 mm. longi.
Corollarum tubi intus ad basim rugis binis ornati; plantae San Luis Potosi, Hidalgo, Mexico, Guanajuato, Tlaxcala et Puebla ..... 224. *S. amarissima.*
Corollarum tubi intus nudi; plantae Oaxaca et Michoacan. 224a. *S. capillosa.*
Corollarum tubi 8–15 mm. longi; plantae guatemalenses vel mexicanae.
Folia utrimque patentim hirsuta et subtus saepius tomentosa; plantae guatemalenses ..... 225. *S. Urica.*
Folia utrimque glabra et viridia, nisi ad venas sparsissime pilosa; plantae mexicanae (Guererro) ..... 225a. *S. sapinea.*
Folia plerumque minus quam 4 cm. longa; petioli rarius plus quam 1 cm.; ramulorum pili magnam partem 1–2 mm. longi.
Ramuli utrimque pilis glandulosis plus minusve vestiti etc. etc.

225. S. Urica Epling. GUATEMALA—CHIQUIMULA: Montaña Nonojá, near Camotán, 600–1800 m., *Steyermark 31697;* Volcan Quezaltepeque, 1500–2000 m., *Steyermark 31493.* JALAPA: Zapote, near San Pedro Pinula, 1500 m., *Steyermark 32958;* Montaña Miramundo, between Jalapa and Lago Ayarza, 2000–2200 m., *Steyermark 32794;* Potrero Carrillo, 13 mi. N. E. of Jalapa, 1500–1700 m., *Steyermark 33129.*

225a. **S. sapinea** Epling, sp. nov. (*Uricae*). Suffrutex altitudine ad 1.5 m. ramulis gracilibus fere glabris tamen pilis longioribus extensis vel recurvis sparse conspersis tamen inter flores brevibus glandulosis et crassioribus dense obsitis; foliorum laminis cordato-ovatis, 6–12 cm. longis, 4–8 cm. latis, in apice breviter et abrupte acuminatis, in basi saepe obliquis, marginibus serratis, pagina superiore fere glabra breviter et sparse hirtella inferiore ad venas pilis longioribus appressis sparsissime ornata, petiolis 3–10 cm. longis, villosis; floribus 6 in verticillastris sat densis bracteis caducis parvis subtentis, glomerulis inter se 1–2 cm. distantibus in spicis interruptis 15–20 cm. longis strictioribus positis; calycibus florentibus purpureis 7–8 mm. longis extus pilis glandulosis brevioribus extensis et paucis crassioribus obsitis, in maturitate paulo auctis; labia superiore 3–5–7-venis; pedicellis 5–6 mm. longis elatis; corollarum violacearum tubo 9–12 mm. longo intus papillis quatuor ornato, labia superiore 4.5–5.5 mm. alta, inferiore duplo longiore.

MEXICO—GUERRERO: Teotepec, distr. Mina, 3375 m., in open pine and fir forest, 6.XI.1939, *Hinton 14798* (TYPE, Univ. Calif., L. A.)

The nature of the stamen connective is somewhat variable. It is usually almost entire or with a slight tooth toward the middle. Occasionally, however, the tooth appears to be somewhat assurgent, in which case the species might be sought under *Fernaldia* (p. 10), from which it may readily be distinguished in a number of ways. If only those calyces which have a 3-veined upper lip are examined, the species would be sought under *Polystachyae*, from which it would be at once distinguished by the size of the corolla, the corolla tubes of that section rarely being over 6 mm. long. See 224a, this paper, for key.

228. S. CORDATA Benth. URUGUAY—SALTO: San Antonio, en cuchillas pedregosas, XI.1937, *Orihuela* (*Rosengurtt 2682*). This species has been known previously only from Rio Grande do Sul.

243a. S. JACOBI Epling. MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 3050 m., *Hinton 14891.*

253. S. RYPARA Briq. This species, predominantly of northwestern Argentina and adjacent Bolivia, may be represented by *Eyerdam 24937*, collected at Cochabamba. Cochabamba, however, is the type locality of *S. platystoma* Epl., known only from specimens collected there by *Bang* (*no. 2032*) and Holway (*no. 386*). The habit, pubescence and flower size of Eyerdam's specimen strongly suggests *S. rypara*, save in the fact that the leaves tend to be deltoid. Whether both supposed species occur there, whether the present specimen is a variant of *S. platystoma* or whether these species are in fact one, is obscure.

267. S. SHANNONI J. D. Smith. GUATEMALA—CHIQUIMULA: Montaña Castilla, near Montaña Cebollas, 3 mi. S. E. of Quezaltepeque, 1200–1500 m., *Steyermark 31220.* On Socorro Mountain between Finca San José and Montaña Nube, 1200–1700 m., *Steyermark 30924.*

273. S. SACCULUS Epling. MEXICO—NUEVO LEON: Below Alamar, about 15 mi. S. W. of Galeana, *Mueller and Mueller 1133.*

281. S. FILIPES Benth. (*S. decora* Epling in Rep. Spec. Nov., Beih. **110**: 222. 1939.) MEXICO—GUERRERO: Armenia Lagunas, 1900 m., Mina, *Hinton 9762;* Puerto Rico, 1800 m., *Hinton 14980;* Chilacayote—Carrizal, 1400 m., *Hinton 14921;* Yesceros—Cruz Pacifica, 2550 m., *Hinton 14900.* The three most recently collected specimens demonstrate the unity of these species, for they seem clearly to connect the two types, separable chiefly because of the narrower leaves, smaller and reflexed flowers of *S. decora.* The flowers may be either white or pale blue.

282. S. PLURISPICATA Epling. MEXICO—MICHOACAN: Mt. Tancitaro, 2850 m., *Hinton 15527.* Although more closely allied by habit to species of *Polystachyae*, as indicated previously, the corolla tubes of this well-marked species are frequently epapillate. Such plants would be sought under *Angulatae.* The styles of the present specimen are glabrous, an unusual condition in the small, blue-flowered sections.

293. **S. pineticola** Epling, sp. nov. (*Carneae*) Herba (?) perennis altitudine 60 cm., caulibus superne pilis decurvis minutis magnam partem eglandulosis pubescentibus, internodiis quam folia brevioribus; foliorum laminis late ovatis, 5–8 cm. diametro, in apice breviter acuminatis, in basi subtruncatis vel leniter cordatis, marginibus convexioribus, serratis, pagina superiore hirtella, inferiore praesertim ad venas pilis crassioribus articulatis sparse villosa; petiolis 5–7 cm. longis; floribus 3–6 in verticillastris bracteis caducis subtentis, in spicis confertioribus 5–15 cm. longis dispositis, glomerulis inter se 5–10 mm. distantibus; pedicellis 3–5 mm. longis; calycibus florentibus tenuibus membranaceis viridibus 5 mm. longis, in maturitate 7 mm. longis, extus glabris, nullomodo glandulosis; corollarum albarum tubo 9 mm. longo, labia superiore 4 mm. alta.

MEXICO—VERA CRUZ: Lomagrande, Mt. Orizaba, 8700 ft., 27.VIII.1938, *Balls 5368* (USNH, TYPE).

In the amended key to the section this species would be sought near 294. *S. gracilis* from which it can be distinguished by the curled eglandular pubescence of the stems, the relatively broad leaf blades, the (? always) white corollas and glabrous, thin calyces which are greenish rather than tinged with red.

294. S. GRACILIS Benth. GUATEMALA—QUEZALTENANGO: Volcan Zanil, 2500–2800 m., *Steyermark 34612.* Calyces nearly 10 mm. long at maturity, 6 mm. in flower. Corolla tubes 12 mm. long, the upper lip 5.5 mm. tall. Otherwise like typical specimens gathered in this vicinity (*Standley 67330*). Specimens recently collected by *Hinton* (*no. 15397*) in Guerrero near Galeana between Piedra Ancha and Tres Cruces may be a white flowered form of this species. The corolla tubes are 11 mm. long, however, and the leaf habit is somewhat different.

299. S. DEBILIS Epling. COLOMBIA—CUNDINAMARCA: Fusagasuga, 2100–2400 m., *Arbelaez and Cuatrecasas 6604;* Mun. Guasca, Paramo de Guasca, 300–3500 m., *Barriga 8093.* This presumed species may have the stems of the inflorescence and calyces minutely glandular, as well as quite glabrous. The habit of foliage is quite variable.

300. S. KILLIPIANA Epling. COLOMBIA—CUNDINAMARCA: Cord, Oriental, Paramo de Guasca, *Cuatrecasas 9445.* The inflorescence is glandular puberulent only.

310. S. ROSCIDA. A specimen collected by *Gentry* (*no. 3651*) in Sonora on Rio Mayo at Curohin apparently is referable to this species and raises the question of the identity of a more recent collection of his, (*no. 5828*) made in Sinaloa, Puerto a Tamiapa. That specimen is seemingly identical with the type of *S. mucidiflora* Fern., described from San Ramon, Durango, except that the villous pubescence of the inflorescence and calyces is almost wholly replaced by small capitate glands. At the same time *S. roscida* seems scarcely different save in flower size from *S. fallax* Fern., described from Tepic. This supposed species has a glabrate analog in Mexia's specimens from Jalisco (*no. 1683*). Furthermore, *S. remissa* Epl., described from Jalisco (*Mexia 1559*) is very similar to *S. fallax*, and specimens recently gathered in Michoacan by *Hinton* (*nos. 12128, 12480, 12357, 12208*), which seem referable to that species, are in turn scarcely to be separated from *S. mucidiflora.* It seems probable, therefore, that *S. mucidiflora* Fern., *S. fallax* Fern., and *S. remissa* Epl. are all referable to *S. roscida* Fern, and form a species which ranges from Durango and southern Sonora to Michoacan. In this species the pubescence of the inflorescence varies from nearly glabrous (*Mexia 1683*) to finely glandular (*Gentry 5828*) or commonly to villous, as in the remaining specimens. The bracts are either deciduous or subpersistent. More abundant collections are needed to reach a decision.

312. S. ARTHROCOMA Fern. MEXICO—VERA CRUZ: Jalapa, San Miguel, 6,500 ft., *Balls 4724.* This specimen appears to be nearest to *S. arthrocoma*, known only from the type locality in Hidalgo, to which it is similar in general habit, the habit of the flowers and pubescence. It has smaller leaves, rounded at the base, and smaller flowers. Jalapa is the type locality of *S. xalapensis,* but the present specimen seems scarcely to be that species.

312b. S. FLACCIDIFOLIA (Angulatae) Fern. in Proc. Am. Acad. **43**: 66.

1908. TYPE: MEXICO—HIDALGO: barranca below Trinidad Iron Works, *Pringle 10298* (Gray).

Herba verisimiliter suffruticosa ramis gracilibus superne hirtellis et plus minusve glandulosis; foliorum laminis sat tenuibus pulchre ovatis, 6–9 cm. longis, 4–6 cm. latis, supra medium acuminatis, etiam subcaudatis, in basi sat rotundatis et cordatis, marginibus serratis, paginis ambabus sparse hirtellis; petiolis gracilibus plerumque 3–6 cm. longis; floribus tribus in bracteorum caducorum axillis, interdum solitariis et oppositis, pedicillis gracilibus 4–5 mm. longis elatis, in racemis laxis 6–8 cm. longis dispositis; calycum florentium tubo 7 mm. longo, extus glanduloso-puberulo, labiis acuminatis; corollarum cyanearum tubo 13–14 mm. longo, galea 9–10 mm. alta.

MEXICO—HIDALGO: Barranca below the Trinidad Iron Works, 6.IX.1906, *Pringle 10298*.

Similar to *S. cyanantha* but the leaves cordate at the base and the flowers somewhat larger and of different conformation. The key to this section is in urgent need of revision, but the material at hand is as yet hardly sufficient. In the present key, this species would probably be sought near *S. myriantha*.

314b. **S. trichopes** Epling, sp. nov. (*Angulatae*). Herba suffruticosa ut videtur ramulis gracillimis glaberrimis; foliorum laminis ovatis, 2.5–4 cm. longis, supra medium acuminatis, in basi rotundatis, marginibus serratis, pagina superiore hirtella vel glabra, inferiore glaberrima; petiolis filiformibus 1.5–2.5 cm. longis; floribus tribus in verticillastris bracteis caducis subtentis, pedicellis gracilibus 3–4 mm. longis elatis; glomerulis laxis inter se 1–2 cm. distantibus in spicis interruptis gracilibus laxis 15–20 cm. longis dispositis; calycibus florentibus 6 mm. longis, sparsissime hirtellis, in maturitate paulo auctis; corollarum rosearum tubo 10 mm. longo, labia superiore 4.5 mm. alta.

PANAMA—CHIRIQUI: in vicinity of Bajo Chorro, 1900 m., *Woodson and Schery 693* (Univ. Calif., L. A., TYPE). Similar in aspect to *S. languidula* of Michoacan and Guerrero, but more glabrous, with larger flowers and deciduous bracts.

339a. **S. cyanicalyx** Epling, sp. nov. (*Angulatae*). Herba perennis altitudine ad 1 m. ramis superne pilis parvis appressis hirtellis, internodiis elongatis quam folia longioribus; foliorum laminis amplis, late ovatis, 8–11 cm. longis, 7–8 cm. latis, in apice breviter acuminatis, acutissimis, in basi rotundatis et ad petiolos abrupte et anguste cuneato-angustatis, marginibus convexioribus, serratis, pagina superiore fere glabra, hirtella, inferiore pilis parvis albo-tomentosa; petiolis 3–4 cm. longis; floribus pluribus in verticillastris, bracteis caducis subtentis, glomerulis inter se 1–5 cm. distantibus in spicis interruptis atro-cyaneis dispositis; calycibus florentibus atro-cyaneis, hirtellis, fere glabris, circiter 9 mm. longis, in maturitate 12 mm. longis 10 mm. latis, labiis hiantibus, acuminatis; corollarum pallide caerulearum tubo sat ventricoso, 12 mm. longo, labia superiore 4–5 mm. alta.

Allied to *S. amplifrons* of Bolivia from which it differs chiefly in the larger corollas and proportionately broader leaves; suggests *S. stachydifolia* (*Malacophyllae*) in habit, but the upper lip of the calyx is definitely 3-veined.

PERU—APURIMAC: Prov. Abancay, Ampuy, 2400–3200 m., 12.II.1939, *Stork, Horton and Vargas 10618* (Field Mus., TYPE).

345. S. AMETHYSTINA J. D. Smith. COLOMBIA—BOYACA: Alto carretera sobre Puente de Boyaca, 2800 m., *Arbelaez and Cuatrecasas 8077*. The upper lip of the calyces is sometimes 5-veined. Furthermore, a fact which I failed to note, the stamens are seated between the middle of the corolla tube and the throat. The general key should accordingly be modified to read as follows (p. 8, line 32):

"H. Stamina vel ad tubi medium vel inter tubi medium et fauces posita. I. Corollae caeruleae infra medium patentim invaginatae 58. *Ampelophyllae*. II. Corollae rubrae vel coccineae integrae 29. *Rubescentes*," and on p. 11, line 5:

"E. Stamina inter corollae tubi medium et fauces posita. F. Corollae labiae breves inferioris lacinia media incurvo-concava (vide etiam *Albolanatas* et *Rubescentes*); tubi integri 91. *Secundae*. FF. Corollae caeruleae labia inferior quam superior longior et patentim deflexa 58. *Ampelophyllae*."

*59a. Nivalis*

Suffrutex ramis gracilibus internodiis sat elongatis foliis deltoideo-ovatis petiolatis; floribus 3–6 in verticillastris bracteis caducis subtentis in spicis interruptis sat confertis dispositis; calycum labia superiore obtusa imprimis 3-venis, interdum 5-venis, inferior pro rata breviore acuminata; corollarum nivearum extus dense albo-hirsutarum tubo intus ad basim papillis quatuor ornato et sub papillas paulo constricto, labiis subaequilongis; staminibus in galea inclusis in faucibus positis, gubernaculo ad connexum dente retrorso ornato; stylo utrimque hirsuto, ramo postico longiore.

351b. **S. Leninae** Epling, sp. nov. (*Nivalis*). Suffrutex altitudine ad 2 m. ramulis pilis extensis vel subretrorsis praesertim ad sulcos ornatis; foliorum laminis deltoideo-ovatis 4–7 cm. longis, 3–5 cm. latis, in apice leniter acuminatis, in basi rotundato-truncatis, paginis ambabus pilis rectis praesertim ad venas sparse conspersis, marginibus serratis; petiolis villosis 1.5–5 cm. longis; calycibus florentibus 8–9 mm. longis ad venas pilis rectis sparse conspersis; corollarum nivearum extus albo-pilosarum tubo 12 mm. longo, labia superiore 8–9 mm. alta, inferiore subaequilonga; staminibus 11–12 mm. longis.

MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 2900 m., in pine-oak forest, 26.XI.1939, *Hinton 14897* (TYPE, Univ. Calif., L. A.).

In the key to the sections this species would probably be sought near *Maxonia*. The key should be amended to read as follows (p. 8, line 1):

"E. Corollarum tubi 6–13 mm. longi; plantae mexicanae et centraliamericanae. F. Folia utrimque angustata; corollae caeruleae vel roseae 59. *Maxonia*. FF. Folia in basi truncato-rotundata; corollae albae albopilosae 59a. *Nivalis*. EE. Corollarum tubi 15–27 mm. long (*S. purpurae* interdum 10–12 mm. longi; vide etiam species colombianam, *S. erythrostoma*). F. Corollae roseo-purpureae vel coccineae. G. Folia in basi saepius rotundata, rarius angustata; 87. *Purpureae*. GG. Folia in basi ad petiolos angustata vel extenuata; corollae coccineae; plantae colombianae 83. *Killipiana*. FF. Corollae cyaneae; plantae guatemalenses 83a. *Latentiflorae*."

If this species is sought in the category in which the upper lip is 5-veined, see under species 224a (p. 560, this paper).

I quote from a letter of transmittal from Mr. James C. Hinton: "If there are any new Salvias in the lot, and if it would be in keeping with the dignity of the subject, I should like to ask you to name a Salvia for my black mule 'Lenina,' which has been in the field for ten years now and has played an indispensable part in the finding of a majority of our new Salvias. Both my father and myself you have already honored. Would it not therefore be just, I ask, to send Lenina's name also down to posterity on some new Salvia?"

I have carefully searched the pages of the International Rules to learn whether there is any prohibition against naming Salvias after mules, but I find none. And what is more deserving of commemoration than the dignity of long and faithful service to science even though it be somewhat unwitting —or sometimes unwilling? Long life to Lenina!

354. S. MEXICANA L. MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 2850 m., Mina, *Hinton 14889;* Petlacala—Buenavista, 2600 m., Mina, *Hinton 14878.* These specimens are apparently referable to the form which was named *S. lupulina* by Fernald. The calyces are broader and the lips relatively shorter. The corollas are somewhat stouter. Branched hairs are frequently seen. The nature of this complex is uncertain, and until much more herbarium material is available for comparison, no certain conclusions can be made. It appears probable, however, that three entities are involved.

379a. **S. betulaefolia** Epling, sp. nov. (*Erythrostachys*). Frutex pulcher ramulis pilis plus minusve retrorsis cinereo-pubescentibus; foliorum laminis deltoideo-ovatis frequenter habitus Betulae, sat tenuibus, 2.5–6 cm. longis, 2–4 cm. latis, supra medium saepius acuminatis et in apice acutis, in basi saepius truncatis, irregulariter dentato-crenatis paginis ambabus pilis extensis sparse pubescentibus; petiolis 1–2 cm. longis; floribus oppositis in paniculis paucifloris brevibus bracteis parvis coloratis perstatis subtentis dispositis; calycibus florentibus pulchre coccineis 16–20 mm. longis, sparse hirtellis, in maturitate paulo auctis subinflatis et infra medium angustatis; corollarum pulchre coccinearum tubo 35–37 mm. longo, labia superiore 16–17 mm. alta.

MEXICO—DURANGO: Tejamen, 21–27.VIII.1906, *E. Palmer 477* (TYPE, USNH); Tepehuanes, 4–25.VI.1906, *E. Palmer 292;* Santiago *Papasquiaro,* 1896, *E. Palmer 404.* CHIHUAHUA: Mojarachic, 6900 ft., 30.VIII.1939, *I. Knobloch 5833.*

A member of the section *Erythrostachys* (no. 379a) and formerly included by me in *S. Regla.* It is more nearly intermediate between *S. Regla* and *S. Sessei.* It may be distinguished from *S. Regla* by the acuminate leaves which are proportionately longer, those of *S. Regla* being broadly deltoid or even reniform, by the more irregular serratures of the leaf margin and by the pubescence, which is not only more abundant but coarser in quality. Just as the leaves of *S. Regla* suggest those of *Populus tremuloides,* the leaves of *S. betulaefolia* suggest those of *Betula alba.*

381. S. SESSEI Benth. MEXICO—MICHOACAN: Zitacuaro to Cayota, 1840 m., *Hinton 13160.*

389. S. SIGUATEPEQUENSIS Standl. GUATEMALA—CHIQUIMULA: Montaña Nube (Volcancitos), southeast of Concepcion de las Minas, 1500–1700 m., *Steyermark 30912; 30913.* Partly intermediate between this species and *S.*

*Karwinskii*. The latter, in typical form, has been collected in Guatemala and it is entirely possible that *S. siguatepequensis* is only a southern phase of it. The calyces are hispidulous and glandular.

390. S. KARWINSKII Benth. MEXICO—CHIAPAS: Volcan Tacana, Chiquihuite, 2800 m., *Matuda 2826*. GUATEMALA—JALAPA: 6 mi. south of Miramundo, Montaña Miramundo, 2000–2500 m., *Steyermark 32705; 32757*. JUTIAPA: Volcan Suchitan 2050 m., *Steyermark 31900*. SAN MARCOS: Volcan Tacana, 2200–2500 m., *Steyermark 36040* (an epiphyte on lower trunk of forest tree).

392. S. WAGNERIANA Polak. GUATEMALA—CHIQUIMULA: Montaña Nube (Montaña Volcancitos), southeast of Concepcion de las Minas, 1500–1700 m., *Steyermark 30916*.

The general key to sections (p. 11, line 32) should be modified to read as follows:

J. Plantae peruvianae; corollarum tubi 13–23 mm. longi 64. *Pavonia*.
JJ. Plantae mexicanae vel centrali-americanae. K. Corollarum caerulearum tubi 3.5–15 mm. longi 43. *Scorodonia*. KK. Corollarum coccinearum tubi 18–25 mm. longi 70. *Cardinales*."

391. S. HOLWAYI Blake. GUATEMALA—CHIQUIMULA: Rio Taco, between Chiquimula and Montaña Barriol, 500–1200 m., *Steyermark 30627*. ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29665*. The leaves of this variable, but readily recognized species, may be as much as 13 cm. long and 8 cm. broad, the petioles being as much as 7 cm. long. The corolla tube may be as short as 15 mm.

401a. S. GRAVIDA Epling. MEXICO—MICHOACAN: Mt. Tancitaro, 2300 m., *Hinton 15677*. The flowers of this species are a beautiful rose-purple. Those of the present specimen appear to be more bluish purple, perhaps due to the accidents of pressing. It is a handsome subject and deserves introduction into our gardens.

410. S. DOMBEYI Epling. PERU—CUZCO: Prov. Paucartambo, near Marcachea, 2400 m., *Vargas 11106*. Described on the label as a tree 3–5 m. tall.

411. S. SCANDENS Epling. PERU—CUZCO: Prov. Quispicanchi, Marcapata, near Chile-Chile, 2000–2500 m., *Vargas 9678*. The type, collected in the same place was said by Weberbauer to be scandent. Apparently it is not always so. It is difficult to determine from the material at hand, but the lower lip of the corolla may be the longer. The species is doubtfully referable to section *Longiflorae*.

420. S. LATENS Benth. (*S. laurifolia* Epling in Rep. Spec. Nov. Beih. **85**: 102. 1936.) COLOMBIA—EL CAUCA: Popayan, Tiembio en Hatoviejo, 1800 m., *Arbelaez* and *Cuatrecasas 6067*. CUNDINAMARCA: Dintel (Facatativa-La Vega), 2700–2800 m., *Arbelaez and Cuatrecasas 5297*. Salto de Tequendama, 2440 m., *Cuatrecasas 8184*.

These proposed species are separable chiefly on the basis of the villous pubescence of the stems and calyces of the former, together with the fact that the flowers are axillary. That both criteria are variable in the type locality is shown by *no. 6067*, and it accordingly seems preferable to consider the species synonymous. Nevertheless, the plants of Cundinamarca appear to

be constantly glabrous. The corollas of *Cuatrecasas 8184* are larger than specimens previously referred here, including the type from the same locality. The corolla tubes are as much as 21 mm., the upper lips 19 mm. and the lower lips 12 mm. long.

*83a. Sect. Latentiflorae.*

Frutices foliis anguste ovatis vel ellipticis in basi angustatis, subcuneatis, breviter petiolatis; floribus in foliorum axillis solitariis in foliis latentibus, ut videtur nullomodo in spicis dispositis; calycibus glabris, labiis acuminatis, superiore 3-venis; corollarum cyanearum tubo superne gradatim ampliato ad basim papillis binis majoribus assurgentibus et binis minoribus retrorsis ornato, nullomodo invaginato, labia superiore erecta, inferiore subaequilonga; staminibus in galea inclusis; stylo piloso, ramo postico longiore; gynobasis cornu ovarium paulo superante. Plants of Guatemala. TYPE SPECIES: *S. opertiflora.*

An amended portion of the key to the sections which includes this section will be found under species 351b (page 565, this paper).

422a. **S. opertiflora** Epling, sp. nov. (*Latentiflorae*). GUATEMALA. Dept. Chiquimula, Volcan Quezaltepeque, *Steyermark 31469* (Field Mus., TYPE.)

Frutex ramulis pilis extensis sat dense et molliter vestitis, internodiis quam folia brevioribus; foliorum laminis ovato-lanceolatis vel ellipticis, 8–9 cm. longis, 2.5–3.5 cm. latis, supra medium leviter acuminatis, in basi angustatis, marginibus serrulatis, pagina superiore viride, sparse hirtella, inferiore pallidiore, sparse villosula, venis purpureis; petiolis obscuris vix 1 cm. longis; floribus paucis axillaribus in foliis latentibus, pedicellis 4–5 mm. longis elatis; calycibus florentibus glaberrimis, pallidis, 12 mm. longis, labiis acuminatis, aequilongis, 4 mm. longis, superiore trivenis; corollarum atropurpurearum vel cyanearum tubo 18–21 mm. longo, habitus S. mexicanae, labia superiore 11–13 mm. alta, inferiore subaequilonga.

GUATEMALA—CHIQUIMULA: Volcan Quezaltepeque, 3–4 miles N. E. of Quezaltepeque, in open thickets, 1500–2000 m., 8.XI.1939, *Steyermark 31469.*

447. S. FLORIDA Benth. PERU—CAJAMARCA: Prov. Cutervo. Trail between Socota and Tambillo, forest of the Ceja de la Montaña, *Stork and Horton 10190.*

The flowering calyces are somewhat smaller (12–13 mm.) than described, and the corolla tube is about 26 mm. long, the stamens being correspondingly smaller. However, there is no doubt as to the identity.

454. S. EXCELSA Benth. GUATEMALA—SAN MARCOS: Volcan Tajumulco, 2300–2800 m., *Steyermark 36599.* First record for Guatemala of this species except the original specimen grown from seeds. See Bull. Torr. Club **67**: 533. 1940. MEXICO—GUERRERO: Paraje Javalin, 2500 m., distr. Mina, *Hinton 15416.*

DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA AT LOS ANGELES

# THE DEVELOPMENT OF THE PERISTOME IN AULACOMNIUM HETEROSTICHUM

H. L. Blomquist and Lora Lee Robertson

(WITH TWENTY-EIGHT FIGURES)

## INTRODUCTION

The peristome is an interesting structure and in the systematics of mosses is considered to be of fundamental importance. The use of the peristome as a character in classification began in 1801 with the publication of Johann Hedwig's *Species Muscorum Frondosorum*, which has been selected as the starting point for nomenclature in the taxonomy of the true mosses. Since that time the establishment of the primary groups of the Bryales has been based alternately upon the peristome, a sporophytic structure, or upon the gametophyte. In recent times, however, owing especially to the influence of the works of Philibert (1884), Fleischer (1900–1922), Goebel (1906, 1930) and others, a more settled opinion has developed among the majority of the students of mosses that the peristome is of the greatest fundamental phylogenetic importance. In the most recent discussion on this subject, Dixon (1932) says, "For one thing it is quite clear that the main types of peristome among the Bryales are of great phylogenetic importance, and are more or less primitive, viz., the Nematodonteae and the Arthrodonteae, the latter divided into Haplolepideae and Diplolepideae. No part of our classification based on gametophyte characters must cut across these broad lines."

In view of this importance of the peristome in the study of mosses, it seems highly desirable that we should have a true concept of what this structure is and some appreciation of its variation in the different groups in which it occurs. Apparently, however, there is a general lack of understanding of what the peristome really is, and this is no doubt partly due to the scarcity of investigations dealing with its development. Furthermore, in some of the few works on this subject, incorrect interpretations add to the confusion.

It is the purpose of this paper to present an account of the embryonal development of a double-peristomate moss which is fairly representative of the diplolepidious Bryales. The main objectives are to show from what embryonic cell-layers a double peristome originates, how it is differentiated, the relation of its mature characteristics to its developmental history, and to correlate it with the peristome of a single-peristomate moss. It is done with the hope that it will lead to a better and wider understanding of this interesting and important structure and will stimulate further investigation.

## HISTORICAL REVIEW

Although Hedwig was the first one to give us any knowledge of the structure of the moss capsule, his concept of the structure of the peristome was far from clear. The first work in which this subject was dealt with more adequately was that of Lantzius-Beninga (1847). The excellency of this contribution has made it a classic in the study of the morphology of mosses. He clearly showed what the peristome is composed of, its unity of plan, and its variation in the several groups which he considered. He was the first one to observe that the peristome is either composed of columns of whole dead cells or of only thickened portions of cells which remain after the surrounding delicate parts break away. Although he worked mainly with mature capsules in which the peristome is fully developed, he observed some of the developmental stages in such genera as *Ceratodon* and *Polytrichum*. Lantzius-Beninga observed the regularity of cell division in the outer region of the operculum, and called attention to the curious fact, which had previously been observed, that the number of parts of the peristome is always four or a multiple of four. He attributed this fact to the regularity of cell division.

Since the appearance of the work of Lantzius-Beninga, the investigations on the peristoma have made some progress along the following more or less distinct lines: (1) comparative morphology of usually mature peristomes from the viewpoint of relationship and phylogeny; (2) its function and behavior; (3) its embryonal development; and (4) its minute structure and chemical composition. Only the last two will be considered here.

The early contributions to our knowledge of the development of the peristome are included in the general investigations concerning the development of the sporophyte as a whole or of the capsule proper. The most important of these is the work of Kienitz-Gerloff (1878) on the development of the sporophyte in several members of the Bryales. He observed, as had Hofmeister (1851), that development proceeds from a two-sided apical cell which cuts off two rows of segments. Each of these segments then divides by an anticlinal wall which results in a column of quadrants of cells. By anticlinal and periclinal cell division the quadrants are further divided into an inner square of four cells and an outer layer of eight cells. The central square, which had been called the "Grundquadrat" by Kühn (1870), Kienitz-Gerloff named the "endothecium" and the outer peripheral layer the "amphithecium." He showed further that the peristome develops from the amphithecium and believed that the basic number of peristome teeth is four.

More special contributions to the development of the peristome were made by Goebel (1887) on *Funaria hygrometrica* Sibth. and *Polytrichum piliferum* Schreb., by Strasburger (1902) on *Mnium hornum* Hedw., and by Campbell (1905) on *Funaria hygrometrica*. All these accounts did not, how-

ever, include the early stages. An account of the development of the capsule of *Ceratodon purpureus* Brid. by Kuntzen (1913) contributed some facts concerning the early stages of the development of the peristome of this moss, although he was mainly concerned with the capsule proper.

The first and one of the few complete accounts of the embryonal development of a peristome in the Bryales is the work by Evans and Hooker (1913) on *Ceratodon purpureus*, a single-peristomate moss. This account is divided into two sections, the first dealing with the development of the peristomial layers and the second with the deposition of the thickenings. They found, as had Kienitz-Gerloff and Kuntzen, that a two-sided apical cell gives rise to two rows of semi-circular segments. After division by an anticlinal wall each pair of alternating segments forms a quadrant of cells. Further division by periclinal walls divides the quadrants into an endothecium of four cells and an amphithecium of eight cells. By periclinal division of the amphithecial cells, two concentric layers of eight cells each are formed, the inner of which becomes the "inner peristomial layer." The cells of the outer amphithecial layer then divide anticlinally and periclinally forming two layers of 16 cells each, and the inner of these becomes the "outer peristomial layer." The cells of this layer divide no further and the number of cells of which it is composed (16) determines the number of peristome teeth. The eight cells of the inner peristomial layer then divide by anticlinal walls in such a way that about three cells of this layer correspond to two cells of the outer peristomial layer. The cells of the outermost layer divide by less regular alternating anticlinal and periclinal walls so that about three layers are formed external to the outer peristomial layer. The innermost of these layers is composed of 32 cells so arranged that two cells correspond with each cell of the outer peristomial layer. The walls upon which deposition takes place to form the peristome teeth are the ones between the outer and inner peristomial layers. Further details concerning the differentiation of the teeth which results in their characteristic form and markings are fully discussed. Some consideration was also given to the statement made by Philibert (1888) that the peristome of a single-peristomate moss is homologous with the inner peristome of a double-peristomate one.

Since the work of Evans and Hooker, a few contributions have appeared dealing with other groups. For the purpose of determining the relationship of the Dawsoniaceae to the Polytrichaceae, Goebel (1906) investigated the peristome in *Dawsonia*. His conclusion that the anomalous peristome of this moss is fundamentally of the same type as in the Polytrichaceae has not, however, been generally accepted. For a similar purpose Goebel (1930) also investigated the development of the peristome in *Diphysium foliosum* Mohr. and *Buxbaumia indusiata* Brid. His conclusion was that the types of peristome present in these mosses indicate no close relationship to the Polytrichaceae as had been formerly supposed.

Working simultaneously but independently van der Wijk (1929) and Lorch (1931) made intensive investigations on the development of the peristome of *Polytrichum*. An additional contribution to the same genus has been made by Wenderoth (1931). Since the type of peristome present in *Polytrichum* has little in common with the type discussed here, a review of their contributions is not considered necessary.

In the work of Lorch, mentioned above, is also a brief contribution dealing with the peristome development of *Mnium cuspidatum* Leyss., a double-peristomate moss. While the early stages are not included, the development of the peristome of this moss up to the stage of the actual differentiation of the peristome teeth may be said to be essentially the same as that of *Ceratodon purpureus* as described by Evans and Hooker. However, since *Mnium* has a double peristome the actual formation of the teeth is quite different from that in *Ceratodon*. The walls upon which the deposit takes place to form the outer peristome are those between the "outer peristomial layer" of Evans and Hooker in *Ceratodon* and the next outer layer of twice as many cells. The inner peristome is formed from the slightly thickened walls between the "outer peristomial layer" and the "inner peristomial layer." In other words, the peristome of *Ceratodon purpureus* develops from the walls which are, with reference to their position, the same as those which develop into the inner peristome of *Mnium cuspidatum*. This fact recalls to mind the statement made by Philibert, mentioned above, concerning the homology of the inner peristome with the peristome of a single peristomate moss. Since in the formation of the double peristome in *Mnium cuspidatum* three layers of cells are involved, Lorch has modified the concept of the peristomial layers as understood by Evans and Hooker. He prefers to consider the innermost peristomial layer which contributes to the secondary thickening of the inner peristome as of a different type from the two succeeding outer layers which he designates as the true ("echte") peristomial layers.

The most recent work on the embryonal development of the peristome is that of Smith (1938) on *Funaria hygrometrica*. This differs from previous work done on this species in that the early stages are included.

The first study of the development of the minute structure of the peristome and its chemical composition was made by Derschau (1900). He concluded that the thickening of the cell wall is by apposition brought about through the activity of both cytoplasm and the nucleus. Cytoplasmic activity governs the first deposit which is largely cellulose and pectin. Later deposits, which are governed by the activity of the nucleus, show a strong reaction with sphagnol which, he concluded, is related to hygroscopic activity and antiseptic property. In the work on the peristome of *Mnium cuspidatum*, Lorch gave considerable attention also to its minute structure.

So far as is known no work has previously been done on the peristome

development in *Aulacomnium heterostichum*. However, Lantzius-Beninga figured transverse and longitudinal sections of the mature peristome of *A. palustre* Schwaegr. (Tab. 62, Figs. 22, 23).

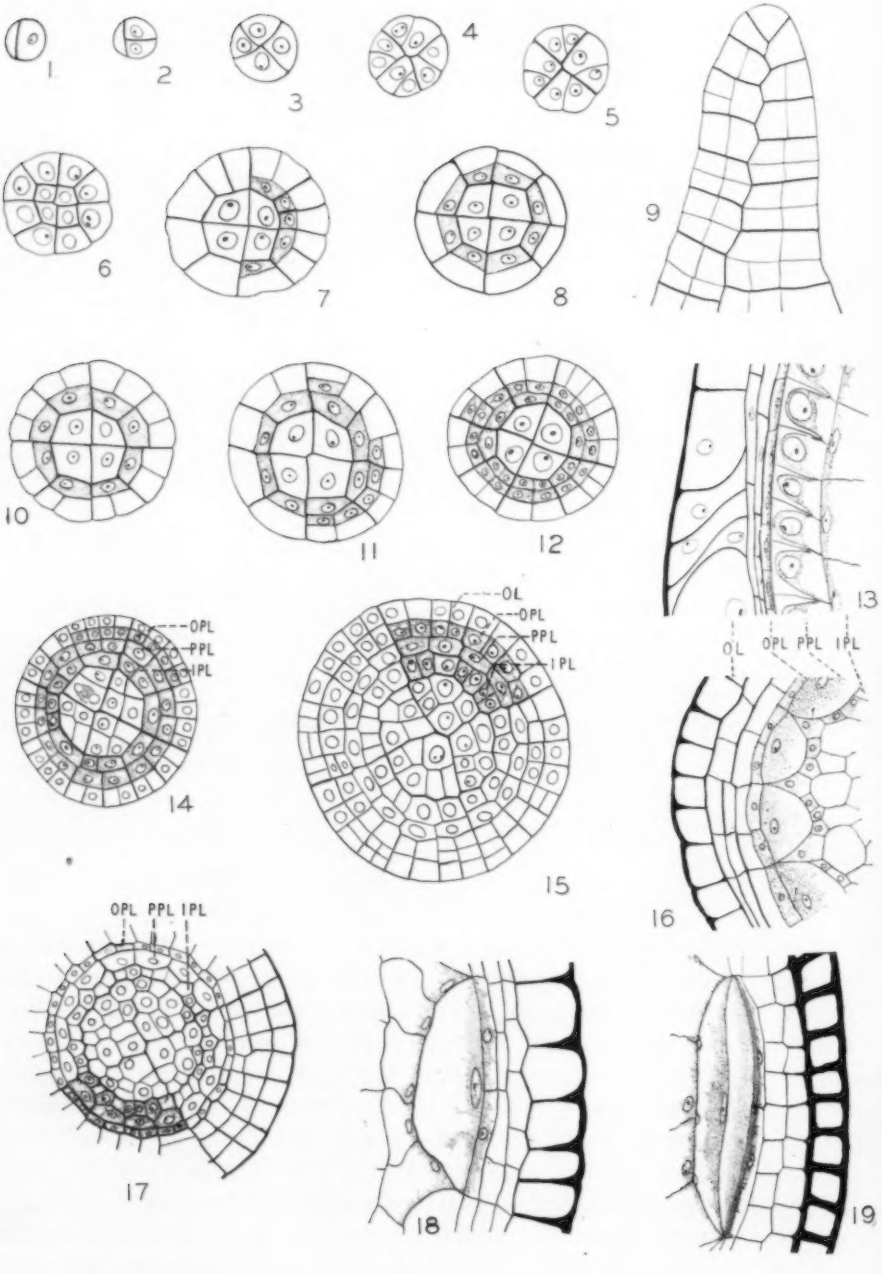
## MATERIALS AND METHODS

*Aulacomnium heterostichum* (Hedw.) B. and S. is a common moss in the vicinity of Durham, North Carolina on shaded river bluffs, associated with other mosses, such as *Bartramia pomiformis* Hedw., *Cirriphyllum Boscii* (Schwaegr.) Grout, *Fissidens cristatus* Wils., and *Hypnum molluscum* Hedw. It is often found growing at the base of trees but it is not confined to this habitat. It is a spring-fruiting perennial which, like other such mosses, produces the sex organs in the spring nearly one year before the sporophyte reaches maturity. Fertilization takes place in the late spring. There seems to be little development of the embryonic sporophyte during the summer months. The sporophytes are first visible with a hand-lens in November. In North Carolina the most rapid growth of the sporophyte takes place during the late winter and early spring. Mature sporophytes are to be found about the middle of April. The peristome is double, consisting of an outer row of sixteen "articulate" teeth and an inner with alternating segments between which are located from two to four well developed cilia. According to the modern systems of classification, its taxonomic position is in the sub-class Bryales, order Eubryales Acrocarpi, and family Aulacomniaceae (Dixon 1932).

Plants were collected when the young sporophytes were first visible with a hand lens. The succeeding collections were made about two weeks apart until spring when collections were made at shorter intervals. Both transverse and longitudinal serial sections were made of the different stages of the developing capsule.

## DEVELOPMENT OF THE PERISTOMIAL LAYERS

The early stages in the development of the sporophyte of *Aulacomnium heterostichum* are essentially the same as in all the Bryales which have been investigated. From the two-sided apical cell, diagonal cell walls cut off alternately semicircular segments (fig. 9). As division continues, the walls separating the older segments are bent down to a horizontal position, leaving the portions below the point where they join in a more or less vertical position (fig. 9). A transverse section of a very young sporophyte, or the tip of an older one, appears as a divided circle (fig. 1). Very soon, however, the alternating semicircular segments are divided radially by vertical walls resulting in a quadrant of cells in transverse view (figs. 2, 3). The cells of these quadrants are then divided by curved anticlinal walls into eight cells (figs. 4, 5). While there is some variation in the way these walls come in, the result is always the same.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The next step is periclinal divisions of the eight cells in such a way that a square of four cells is formed in the center surrounded by a layer of eight cells (fig. 6). The central group of four cells is the endothecium and the outer layer of eight cells the amphithecium. These two groups of cells are the fundamental embryonic layers in the sporophyte of mosses. Below the region of the operculum, the endothecium gives rise to the columella, the inner sporesac, and the archesporium; the amphithecium gives rise to the outer sporesac, the air spaces and the outside layers of the capsule proper (fig. 20). In the region of the operculum the endothecium consists of undifferentiated cells representing extensions of the regions in the capsule proper, but the amphithecium gives rise to the peristomial layers and the operculum. Since this paper is concerned mainly with the peristomial layers, not much attention will be given to the rest of the capsule.

Further development from the fundamental embryonic layers as shown in figure 6 proceeds with striking regularity in the three planes. Since the most important development takes place radially, most attention has been devoted to transverse sections. The regularity in development has two aspects. First, when a cell in a certain pericentral layer divides in a certain plane, all cells in that layer divide in the same plane at about the same time. Second, there is a regular alternation between periclinal and anticlinal divisions. That is, after a cell has divided periclinally the outer of the two daughter cells divides anticlinally. The result is that any layer of cells in the amphithecium has twice as many cells as the next inner layer. This regularity of cell division was called by Goebel the "Grundquadrat" or "fundamental square" method. As was pointed out by Kienitz-Gerloff, since all layers develop with this regularity of cell division from an original group of four cells, the result is that the number of cells in each pericentral layer will be a multiple of four. Furthermore, since the number of peristome teeth depends upon the number of cells making up a certain peristomial layer, the number of peristome teeth will also be of this series of numbers.

Going back to the fundamental embryonic layers, development is seen to proceed from them first by periclinal division of the cells in the amphi-

**Explanation of figures 1–19**

All figures have been drawn with the aid of a camera lucida at the following magnifications: figures 1–25, × 415; figures 26–28, × 155.

The following abbreviations are used: OL, opercular layer; OPL, outer peristomial layer; PPL, primary peristomial layer: IPL, inner peristomial layer; SL, spore layer.

FIGS. 1–6. Successive stages in the development of the endothecium and amphithecium. FIGS. 7–8, 10–12, 14–17. Successive stages in the development of the peristomial layers. FIG. 9. Longitudinal section of a tip of a young sporophyte. FIG. 13. Longitudinal section of an immature peristome. FIG. 16. Transverse section of a peristome just before commencement of secondary thickening. FIG. 18. Commencement of secondary thickening of cell walls forming the peristome in the region of the annulus. FIG. 19. Advanced stage in the differentiation of the peristome.

thecium, resulting in two concentric layers of eight cells each (figs. 7, 8). The cells of the outer layer next divide anticlinally giving rise to 16 cells (fig. 10). This is followed by periclinal divisions in this layer giving rise to two concentric layers of 16 cells each (figs. 11, 12). Again the outer of these two layers divide anticlinally so that 32 cells are formed and these are divided periclinally into two outermost layers of 32 cells each (figs. 14, 15).

At this stage (fig. 15) the amphithecium is, therefore, composed of four concentric cell-layers. These layers will be referred to respectively, starting from the inside, as the inner peristomial layer (IPL), the primary peristomial layer (PPL), the outer peristomial layer (OPL), and the opercular layer (OL).

In the inner peristomial layer, which was originally composed of eight cells, the number of cells has increased by anticlinal divisions (fig. 15). The method of cell division and the ultimate number of cells in this layer will be discussed later. Since this layer contributes to peristome formation it was called by Evans and Hooker the "inner peristomial layer" and for the same reason has been so designated in this discussion.

The primary peristomial layer is composed of 16 cells which divide no further. They enlarge rapidly and their inside walls soon become distinctly convex (figs. 16, 17). This is, therefore, the first peristomial layer to appear conspicuously different from the other layers. For this reason and because, as will be shown later, the number of cells of which it is composed determines the number of teeth, it seems desirable to designate this layer as the *primary peristomial layer*. The cells of which it is composed will be referred to as the *primary peristomial cells*. This layer was called the "outer peristomial layer" by Evans and Hooker and the inner of the two "echte" peristomial layers by Lorch.

The cells of the outer peristomial layer are 32 in number and they divide no further. Their enlargement is almost entirely in a tangential direction. The cells of this layer also contribute to peristome formation, and for this reason it is called the *outer peristomial layer*. It is the outer of the two "echte" peristomial layers of Lorch. Since this layer does not participate in peristome formation in a single-peristomate moss such as *Ceratodon*, it was not given any special designation by Evans and Hooker.

The opercular layer, which at this stage consists of 32 cells, does not contribute to peristome formation. As in *Ceratodon* and other genera investigated, the cells of this layer continue dividing by a less regular alternation of periclinal and anticlinal divisions than is exhibited by the cells of the other layers, resulting in the formation of about three layers external to the outer peristomial layer (fig. 17). The outermost one of these differentiates into the operculum.

It must be realized, of course, that in the development of the sporophyte,

growth soon ceases in the apical embryonic region, leaving the tip conical in form. This is partly responsible for the triangular shape of the peristome teeth.

### THE DEVELOPMENT OF THE INNER PERISTOME

The inner peristome, also called the endostome, develops from the cell walls between the inner and the primary peristomial layers. As was stated above, the original eight cells of the inner peristomial layer at a certain stage (fig. 15) commence dividing anticlinally. The first division is usually such that one of the daughter cells is smaller than the other (fig. 15). The larger of the two then divides so that from the original cell three cells are formed which subtend two cells of the primary layer. This is exactly what Evans and Hooker found in *Ceratodon purpureus* but with this important difference, that in *Ceratodon* division goes no further while in *Aulacomnium heterostichum* division continues until eight or nine cells of the inner peristomial layer subtend two of the primary (figs. 16, 18, 19). In *Mnium cuspidatum*, Lorch found a similar arrangement. In *Funaria hygrometrica*, Smith shows only four cells of the inner layer subtending two of the outer. However, in the illustrations of this species given by Lantzius-Beninga (Tab. 63, Figs. 25, 27) the number varies from four to six, apparently depending upon the level of the operculum at which the sections are made.

As shown above, the inner walls of the primary peristomial cells become distinctly convex (fig. 17). The cause of this convexity is no doubt a combination of growth factors. Perhaps the most important of these is the formation of a larger number of cells subtending one primary peristomial cell in the inner peristomial layer than is formed in the outer peristomial layer. This at least partial explanation is supported by the fact that in such forms as *Ceratodon* and *Funaria*, in which the number of cells in the inner and outer peristomial layers subtending one primary peristomial cell is about the same, little or no convexity is exhibited by the primary peristomial cells. Other factors may be the position of the radial walls of the inner peristomial layer with refereince to the radial walls of the primary peristomial cells, and the higher turgor pressure of the primary peristomial cells than that which obtains in the cells of the inner peristomial cells. One result of this convexity is the formation of wedge-shaped cells in the inner peristomial layer between the primary peristomial cells. The two walls of these wedge-shaped cells contiguous with portions of the inner walls of the primary peristomial cells form the "keels" of the "segments" of the inner peristome (figs. 16, 18, 19).

The commencement of deposition in the differentiation of the inner peristome is indicated by the migration of cytoplasm and nuclei of the inner peristomial layer toward the outer walls of these cells (figs. 16, 18, 19). Little if any secondary thickening apparently takes place on the contiguous

inner walls of the primary peristomial cells. The deposit of the inner peristome is scanty and of homogeneous structure except in the upper portions where it is distinctly spicular (fig. 23). In the lower half of the inner peristome the deposit is continuous between the tangential walls, and the vertical rows of walls of this portion do not, therefore, separate. This basal portion of the inner peristome is known as the "basilar membrane" (fig. 28). In the upper half, however, no secondary thickening takes place at the junction of the tangential walls, which therefore separate in vertical strips except at the tips of the keels (figs. 23, 28). The narrow vertical strips between the keels are the "cilia," which vary in *Aulacomnium heterostichum* from two to four. No pores develop in the segments of this species like those noted by Lorch in *Mnium cuspidatum*.

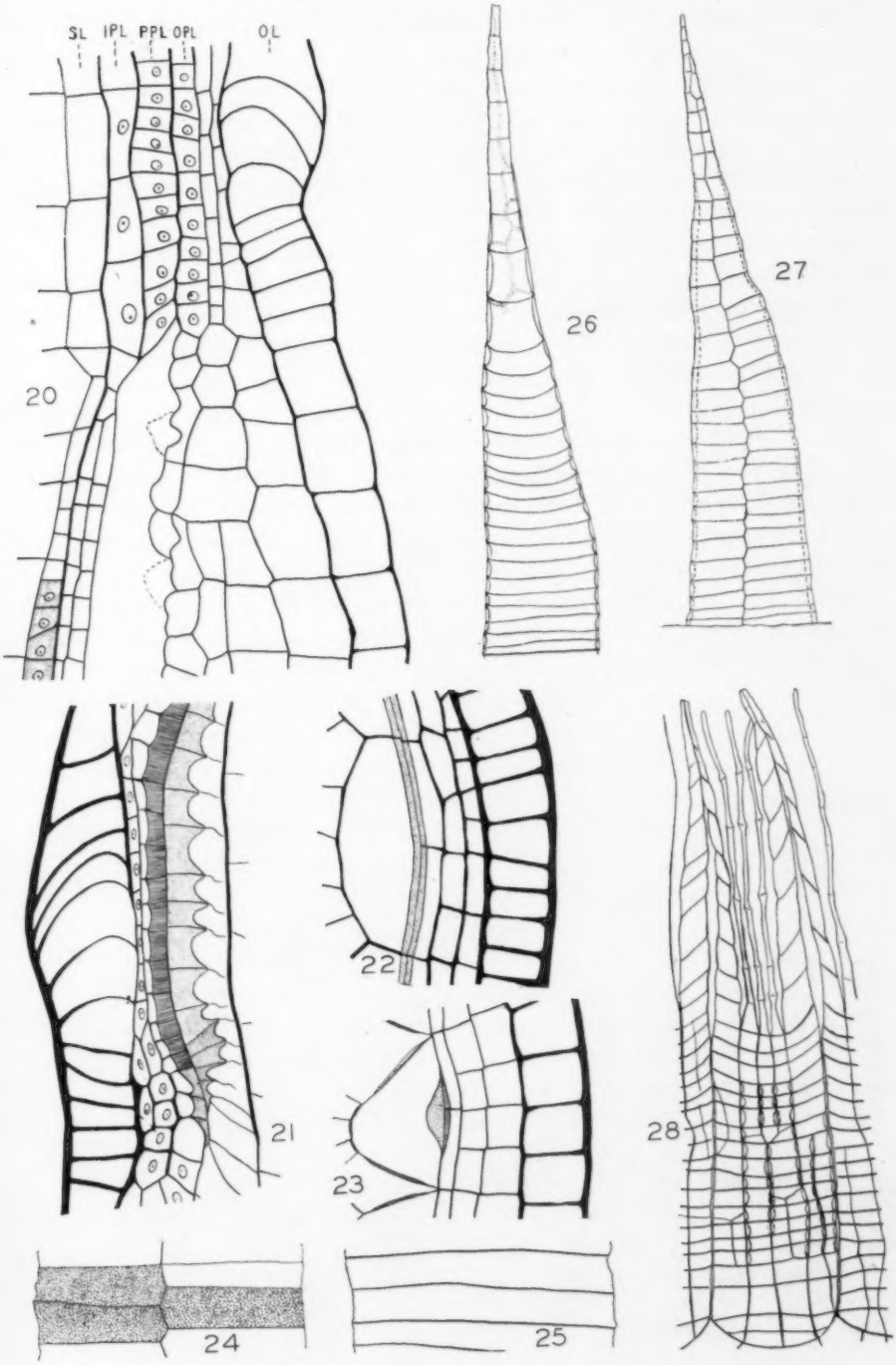
On the outside of the lower half of the endostome, rows of curious button-like elevations are to be seen along the vertical walls between the radial horizontal walls (figs. 19, 28). So far as known these elevations have not been noted before in this or any other species.

### THE DEVELOPMENT OF THE OUTER PERISTOME

The outer peristome (the exostome) develops from the walls between the primary peristomial cells and the cells of the outer peristomial layer. It will be recalled that each primary peristomial cell subtends two cells of the outer peristomial layer. Here, as in the inner peristome, the first indication of secondary thickening is the migration of the cytoplasm and the nuclei toward the walls on which deposition will take place. Since in this case deposition takes place on both walls, the cytoplasm and nuclei in the primary peristomial cells move outward and in the outer peristomial layer they move inward (fig. 18). The deposit made by the primary peristomial cells is copious and, as observed by Lorch in *Mnium cuspidatum*, quite homogeneous in structure although somewhat stratified (fig. 19). This deposit is not confined to the tangential walls but extends considerably over the horizontal radial walls as seen in figure 13. The large size of the nuclei in this figure indicates incipient disintegration. The deposit on the outside of the outer peristome is of an entirely different structure from that on the inside, being distinctly spicular (fig. 19). The same types of deposit were also noted by Lorch in *Mnium cuspidatum*. A longitudinal section through a mature tooth

**Explanation of figures 20–28**

FIG. 20. Longitudinal section of a young capsule showing relation of peristomial layers to the outer regions of the capsule proper. FIG. 21. Longitudinal section of the basal region of the peristome. FIG. 22. Transverse section of the basal region of the peristome. FIG. 23. Transverse section of upper region of nearly mature peristome. FIG. 24. Outside view of portion of outer peristome. FIG. 25. Inside view of portion of outer peristome. FIGS. 26–27. Inner and outer views respectively of an outer peristome tooth. FIG. 28. Portion of inner peristome viewed from inside.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is shown in figure 21. In *Ceratodon purpureus* Evans and Hooker found that the deposits on the two sides were essentially the same except that it was thicker and less uniform on the outside. In *Ceratodon* the early deposit is homogeneous but the later deposit is distinctly spicular on both sides. Since no deposition takes place at the junction of the vertical radial walls separating the primary peristomial cells and the walls of the outer peristome, except at the base, the peristome teeth separate at maturity.

As seen in figure 21 the peristome extends a considerable distance below the annulus. For a distance of about three cells from the base the deposit is the same on both sides, being homogeneous in structure. Between this portion and the cells of the operculum is a group of cells with somewhat thickened cell walls which apparently supports the peristome and acts as a hinge.

In the basal part of the outer peristome the deposit is continuous on both sides from tooth to tooth (fig. 22). This continuity of deposit decreases upward so that at the tip of the teeth it occupies only a narrow strip in the middle of the tangential cell walls (fig. 23). This condition contributes to the triangular shape of the teeth.

Since the form and markings of the peristome are of taxonomic importance it might be profitable to show their developmental relationship. Looking at the outside of a mature peristome tooth it will be seen that it is divided down the center by a somewhat zigzag line from which alternating lines extend out horizontally to the margins (figs. 24, 27). These lines represent the bases of the cell walls of the outer peristomial layer in which, it will be recalled, two cells subtend one cell in the primary peristomial layer. The margins show a narrow transparent strip due to the sparsity of secondary thickening along the edges. The inside view of a peristome tooth shows the absence of a vertical median line because this wall is only one cell wide. The horizontal lines represent, of course, the remnants of the horizontal radial walls (figs. 25, 26). In the upper portion, the outside median line may be visible because of the sparsity of secondary thickening in this portion.

The portion of the inner peristome which extends between two keels is subtended by one outer peristome tooth (fig. 28). Since the wall making up the outside of this portion of the inner peristome is the inner wall of a primary peristomial cell, the markings will correspond with those of the inside of the outer peristome tooth. However, owing to the lack of secondary thickening on this side, the cell outlines are very faint. The inside of the inner peristome shows from three to five vertical lines which represent the bases of the vertical radial cell walls. The horizontal lines represent the transverse radial walls. Occasionally extra lines appear which indicate irregularities in cell division.

## DISCUSSION

In comparing the various accounts on peristome development, it is obvious that there are some differences of interpretation. These differences are concerned mainly with (1) the position of the inner peristomial layer with reference to the endothecium and (2) the relation of the peristome of a single peristomate moss to that of a double one.

Van der Wijk (1932, p. 34) in referring to Lantzius-Beninga's figure of *Hypnum silvaticum* (Tab. 65, Fig. 30) interprets the walls which develop into the inner peristome as the borderline between the endothecium and amphithecium. The similarity between the mature peristome of this species as shown by the above figure and *Aulacomnium heterostichum* would indicate that this is a misinterpretation. From all the accounts which have included the early stages of development, it is clear that the walls which form the inner peristome are between the first and the second cell layers *outside* of the endothecium.

Another interpretation somewhat similar to the above was made by Lorch in discussing *Mnium cuspidatum* (p. 249). He considers the position of the inner peristome as the outside limit of the columella. Since the outside limit of the columella in the region of the capsule is several cell layers within the cell layers which, projecting up into the region of the operculum, develop into the inner peristome, it is confusing to consider the limit of the columella as forming the inner peristome. Of course it is possible that his interpretation of the columella is different in the two regions.

In the account of the development of the peristome of *Ceratodon purpureus*, Evans and Hooker clearly show the relation between a single peristome and a double one. In all the cases investigated a single peristome develops from the walls between the innermost layer of cells of the amphithecium (IPL) and the next outer layer which in the present paper has been designated as the "primary peristomial layer" (PPL). Smith (1938, p. 101), however, in comparing the peristome of *Funaria* with that of *Ceratodon*, apparently misinterprets the position of the peristome of the latter, although his statement is not clear. He says: "Other genera, as *Ceratodon*, have a thickening of outer tangential walls only in the outer layer of the peristome."

To avoid confusion in interpretation it is suggested here that the same terminology be applied to the peristomial layers in both Haplolepideae and Diplolepideae. This is possible because from the evidence gathered from all accounts dealing with typical forms belonging to the Bryales, the peristomial layers are similar and have the same relative position in both the single- and double-peristomate forms. The principal variation is in the number of cells composing the layers, and in the number of cell-layers outside of the peristomial layers which, however, may vary to some extent at different levels of the operculum.

The conclusion of Philibert that a single peristome is homologous with the inner peristome of a double one seems to be true for the forms so far investigated if homology refers only to the primary cell walls. However, if our concept of homology includes the secondary thickening, which is after all the most important feature in peristome differentiation, his statement becomes only half true. According to Evans and Hooker both the inner and primary (the "outer") peristomial cell layers contribute to secondary thickening in a single peristome but in a double one, such as that of *Aulacomnium heterostichum*, only the inner peristomial layer contributes to the inner peristome.

The regularity of cell division and its significance in the development of the peristomial layers has been emphasized in this account as in all previous ones. That there is a striking regularity is undoubtedly true, but exceptions occur. Van der Wijk in his work on *Polytrichum* observed irregularities which even altered the number of teeth from the usual number of 64. In *Aulacomnium heterostichum* also some irregularities occur. As mentioned above, irregularities appear in the formation of the layers outside of the peristomial layers. The result is that the number of these layers varies to some extent vertically and the number of cells of which each is composed may not conform to the results expected from the fundamental square method. Even in the formation of the peristomial layers slight variations may occur. As is shown in figure 12 an anticlinal division may be occasionally duplicated in a corresponding cell of the next inner layer. Also anticlinal or periclinal divisions may take place out of turn centrifugally (fig. 15) but, so far as has been observed, the final result is always the same. In no instance has the number of peristome teeth been found to vary from the usual number of 16. In the inner peristomial layer, considerable variation takes place in all three planes. The most important of these variations concerns the number of vertical radial walls in the upper portion. The result is that the number of cilia varies from two to four. This fact is of some importance since they often enter into taxonomic considerations.

## SUMMARY

1. The peristome of *Aulacomnium heterostichum* originates from the outer of the two fundamental layers in the opercular region of the sporophyte. This layer, which is called the amphithecium, is originally composed of eight cells.

2. By a regular alternation of periclinal and anticlinal cell divisions the amphithecium develops into six concentric layers, each of which has twice as many cells as the next inner layer. The number of cells in each layer is a multiple of four.

3. The double peristome is formed from the three innermost cell layers of the amphithecium.

4. Differentiation is initiated by the enlargement of the 16 cells of the middle of the three peristomial layers. Since the cells of this layer contribute more than those of the other layers to peristome formation and their number determines the number of peristome teeth, it is called the *primary peristome layer*.

5. The layer outside of the primary peristomial layer, which also contributes to peristome formation, is called the *outer peristomial layer*. Two cells of this layer subtend one cell of the primary peristomial layer.

6. The innermost layer contributes to the formation of the inner and is, therefore, called the *inner peristomial layer*. Since this layer is ultimately composed of from 64 to 72 cells, eight or nine cells of this layer subtend one cell of the primary.

7. The outer peristome is formed from a deposit of cell wall material laid down on the outer tangential cell walls of the primary peristomial layer contiguous to another deposit laid down on the inner tangential walls of the outer peristomial layer. The deposit on the inside is homogeneous while that on the outside is spicular.

8. The inner peristome is formed from the original inner tangential walls of the cells of the primary peristomial layer and the contiguous outer tangential walls of the inner layer. Only the cells of the inner peristomial layer contribute a deposit to the inner peristome.

9. The keeled condition of the segments of the inner peristome is due to the convexity of the inner walls of the primary peristomial layer.

10. Owing to the lack of deposit at the junction of the radial and tangential walls in the upper region of the inner peristomial layer, strips of cell plates separate to form from two to four cilia. This variation in the number of cilia is due to the variation in the number of cells in the inner peristomial layer subtending one cell in the primary.

11. The development of the peristome in *Aulacomnium heterostichum* is compared with the development of the peristome of other genera of mosses investigated.

12. The peristome of a single-peristomate moss develops in the same position with reference to the cell layers as the inner peristome of a double-peristomate moss.

13. It is suggested that to avoid misinterpretation the same terminology be applied to the peristomial layers in both the single- and double-peristomate mosses.

14. Some of the irregularities in peristome development are discussed.

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## Literature Cited

**Campbell, D. H.** 1905. The Structure and Development of the Mosses and Ferns. 2nd ed. New York.

**Derschau, M. van.** 1900. Die Entwickelung der Peristomzähne des Laubmoossporogoniums. Bot. Centralbl. **82:** 161–168, 193–200.

**Dixon, H. N.** 1932. Classification of Mosses. *In* Verdoorn, F. Manual of Bryology, 397–412.

**Evans, A. W. & Hooker, H. D.** 1913. Development of the peristome in *Ceratodon purpureus*. Bull. Torrey Club **40:** 97–109.

**Fleischer, M.** 1900–1922. Die Musci der Flora von Buitenzorg. Leiden.

**Goebel, K.** 1887. Outlines of Classification and Special Morphology of Plants. (English translation.) Oxford.

————. 1906. Archegoniatenstudien. X. Beiträge zur Kenntnis australischer und neuseeländischer Bryophyten. Flora **96:** 1–202.

————. 1930. Organographie der Pflanzen. 2. Bryophyten und Pteridophyten. 3rd. ed. Jena.

**Hedwig, Johann.** 1801. Species Muscorum Frondosorum. Leipzig.

**Hofmeister, W.** 1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen. Leipzig.

**Kienitz-Gerloff, F.** 1878. Untersuchungen über die Entwickelungsgeschichte der Laubmoos-Kapsel und die Embryo-Entwickelung einiger Polypodiaceen. Bot. Zeit. **36:** 33–64.

**Kühn, E.** 1870. Zur Entwickelungsgeschichte der Andreaeaceen. *In* Schenk, A. & Lürssen, C. Mittheilungen aus der Gesamtgebiete der Botanik **1:** 1–56.

**Kuntzen, H.** 1913. Entwickelungsgeschichte des Sporogons von *Ceratodon purpureus*. Inaug. Diss. Berlin.

**Lantzius-Beninga, S.** 1847. Beiträge zur Kenntniss des innern Baues der ausgewachsenen Mooskapsel, insbesondere des Peristoms. Nova Acta Acad. Leop.-Carol. **22:** 555–604.

**Lorch, W.** 1931. Anatomie der Laubmoose. *In* Linsbauer, K. Handbuch der Pflanzenanatomie **7**[1]: 1–358.

**Philibert, H.** 1884. De l'importance du péristome pour les affinités naturelles des mousses. Rev. Bryol. **11:** 49–52, 65–72.

————. 1888. Etudes sur le péristome. Rev. Bryol. **15:** 6–12, 24–28, 27–44, 50–60, 65–69.

**Smith, G. M.** 1938. Cryptogamic Botany **2:** 107–109. New York.

**Strasburger, E.** 1902. Das botanische Practicum. 4th ed. Jena.

**Wenderoth, H.** 1931. Beiträge zur Kenntnis des Sporophyten von *Polytrichum juniperinum* Willdenow. Planta **14:** 244–385.

**Wijk, R. van der.** 1929. Ueber den Bau und die Entwicklung der Peristomzähne bei *Polytrichum*. Rec. Trav. Bot. Néerl. **26:** 289–395.

————. 1932. Morphologie und Anatomie der Musci. *In* Verdoorn, F. Manual of Bryology, 34.

# STUDIES ON THE EMBRYO OF HORDEUM SATIVUM—I. THE DEVELOPMENT OF THE EMBRYO

JAMES MERRY

(WITH FORTY-TWO FIGURES)

## INTRODUCTION

Studies on the morphology of grass embryos have been based on observations either of embryos in early stages of development or of embryos and seedlings of mature seeds. In the first the gross morphological development was described and in the second the vascular anatomy of the embryo was given. The object of undertaking the work presented here was to describe the development of the embryo from the time of fertilization to the maturation of the ovule into a seed, and to give not only the development of the gross differentiation but that of the internal differentiation as well. To accomplish this a conventional histological study was made of the normal embryo at daily stages of development, and in addition the study of the vascular differentiation was aided by the use of the technique of growing excised embryos on an artificial medium.

When whole embryos are grown on an artificial medium small plants resembling seedlings are produced. The cells of the embryo which are potentially vascular tissue become more clearly differentiated in the cultured plant. Because of this vascular differentiation the cultured plants were found useful in studying the development of the normal embryo. The more developed the embryo is, the greater is the amount of internal differentiation in the plant grown from it. Thus the cultured plants show the potential differentiation which is not clearly visible in the normal embryos.

## HISTORICAL SURVEY

It is proposed to give the historical origin of some of the terms commonly used in reference to grass embryos and to summarize the controversial views regarding grass embryo morphology for the benefit of those who may not be familiar with the extensive literature. For more detailed reviews of certain phases of embryo morphology the reader is referred to Van Tieghem (1872), Bruns (1892), Avery (1930), Randolph (1936), and McCall (1934).

According to Van Tieghem (1872) and others the earliest description of the embryo of grasses is that by Malphigi in 1687 of the embryos of *Avena* and *Triticum*, in which he recognized the structures now known as the scutellum, epiblast, and coleoptile. Gaertner has been credited with the first use of the term scutellum which is still commonly applied to the shield-shaped structure characteristic of the grass embryo. Richard in 1813, accord-

ing to Van Tieghem (1872), originated the term blast for that part of the embryo which becomes the stem of the plant, and from this he developed the term hypoblast for the scutellum. The small projection found on the outer face of some grass embryos was correspondingly called the epiblast, a term which is still in common use. The term blast itself has been displaced in English by plumule. Richard used the term cotyledon for the sheath around the blast, which Van Tieghem (1872) said was first given the present name, coleoptile, by Mirbel in 1815. The lower portion of the embryo has received less attention than the parts mentioned above, since there is little question about its homologies. The term radicle is used for that part of the embryo which becomes the primary root, and the surrounding tissue is called the coleorhiza. The term seminal roots has been used to include the radicle or primary root and any other roots present in the embryo. The argument over the homology of the scutellum has caused much difference of opinion as to what the region between the coleoptile and the scutellum actually is. In embryos such as those of *Avena* or *Zea* this region is of considerable extent. Van Tieghem (1872) considered that this was the node of the scutellum but later changed his views on the homologies of the embryo and called this region an internode (1897) between the scutellum as one leaf and the coleoptile as a second, as had Bruns in 1892. Čelakovský (1897) introduced the term mesocotyl for this part of the embryo because of his conclusion that the scutellum and the coleoptile together made up the cotyledon. The term mesocotyl has been commonly used, though the term "first internode" is now used by many workers who are interested in the growth of this part of the *Avena* seedling and who consider the scutellum and the coleoptile to be separate leaves.

The most debated points in the morphology of the grass embryo are the homologies of the scutellum, epiblast, and coleoptile, on which there seem to be three main views. The first considers the scutellum to be the first leaf, that is, the cotyledon of the embryo, and the coleoptile to be the first leaf of the plumule. The second view holds that the coleoptile is the cotyledon and that the scutellum is an outgrowth of the radicle or stem. The third view is that the scutellum and the coleoptile together make up the first leaf, that is, the cotyledon. A variation of the first view is that the scutellum is the first leaf, the epiblast the second leaf, and the coleoptile the third leaf of the plant. The papers already cited give a more complete development of these views.

The early studies on the formation and development of the embryo were based mostly on observation of whole embryos. Norner (1881) studied the early divisions of the zygote and proembryo of *Hordeum*, *Avena*, *Triticum*, and *Secale* by dissecting out whole embryos and mounting them in glycerine for observation. The oldest stages of which he gave figures were just beginning to show gross differentiation. He attempted to classify the arrangement of the cells according to the manner in which they divided, but the irregu-

larity of the arrangement as shown by his figures would not seem to warrant this. Čelakovský (1897) showed five stages in the development of the upper part of the embryo to prove that the coleoptile is part of the scutellum. He did not identify the drawings by species, but stated that they were for the most part after Hanstein's figures.

Souèges (1924) traced the parts of the fully developed embryo of *Poa annua* back to the tiers of cells in the sixteen-celled proembryo. He also indicated that there was a definite arrangement of the cells and a regular sequence of cell divisions in the development from the fertilized egg. He maintained that the parts of the embryo are determined at least as early as the sixteen-celled stage. Randolph (1936) has given the only complete description of the development of a grass embryo in which the age of the various stages was determined. In the development of the embryo of *Zea* he found that there was no definite arrangement of the cells nor any regular sequence of divisions in the early stages.

## MATERIAL AND METHODS

*Hordeum sativum* L. was chosen for this work because it is easy to grow in the greenhouse and a relatively large number of grains of the same age can be obtained from one head. Also, embryos of *Hordeum* varying as little as one day in age show recognizable morphological differences. A variety alpha, obtained from the College of Agriculture, Cornell University, was used for the work presented here. All the plants from which material was taken were grown in the greenhouse both in winter and summer.

The heads of the plants were examined several times a week and were tagged when the anthers had split. Two florets were fixed at this time and sectioned to determine when fertilization had occurred or would occur. At a selected time after tagging a head was picked and two or three ovules fixed for the study of normal development. All material was fixed in a solution of 50 per cent alcohol, 6 per cent formalin, and 6 per cent acetic acid. The normal embryos large enough to be removed from the ovules and plants cultured from the embryos were cleared and mounted in xylene in deep well slides and studied as temporary mounts. Camera lucida drawings were made from these mounts for record purposes. This material was of course taken into paraffin from the xylene. The rest of the material was run up to paraffin from the fixing solution by a short dioxane series. Sections 10 μ thick were made of the embedded material and stained in safranin and Delafield's haematoxylin. Measurements were made with an ocular micrometer both from temporary mounts and sections.

## DESCRIPTION

In presenting the development of the embryo the various parts are treated separately except for the early stages or that phase of the develop-

ment usually referred to as the proembryo. The differentiation of each structure, the manner in which it develops, and the differentiation of its vascular system are described. Also the vascular connection between the primary root and the rest of the embryo is traced.

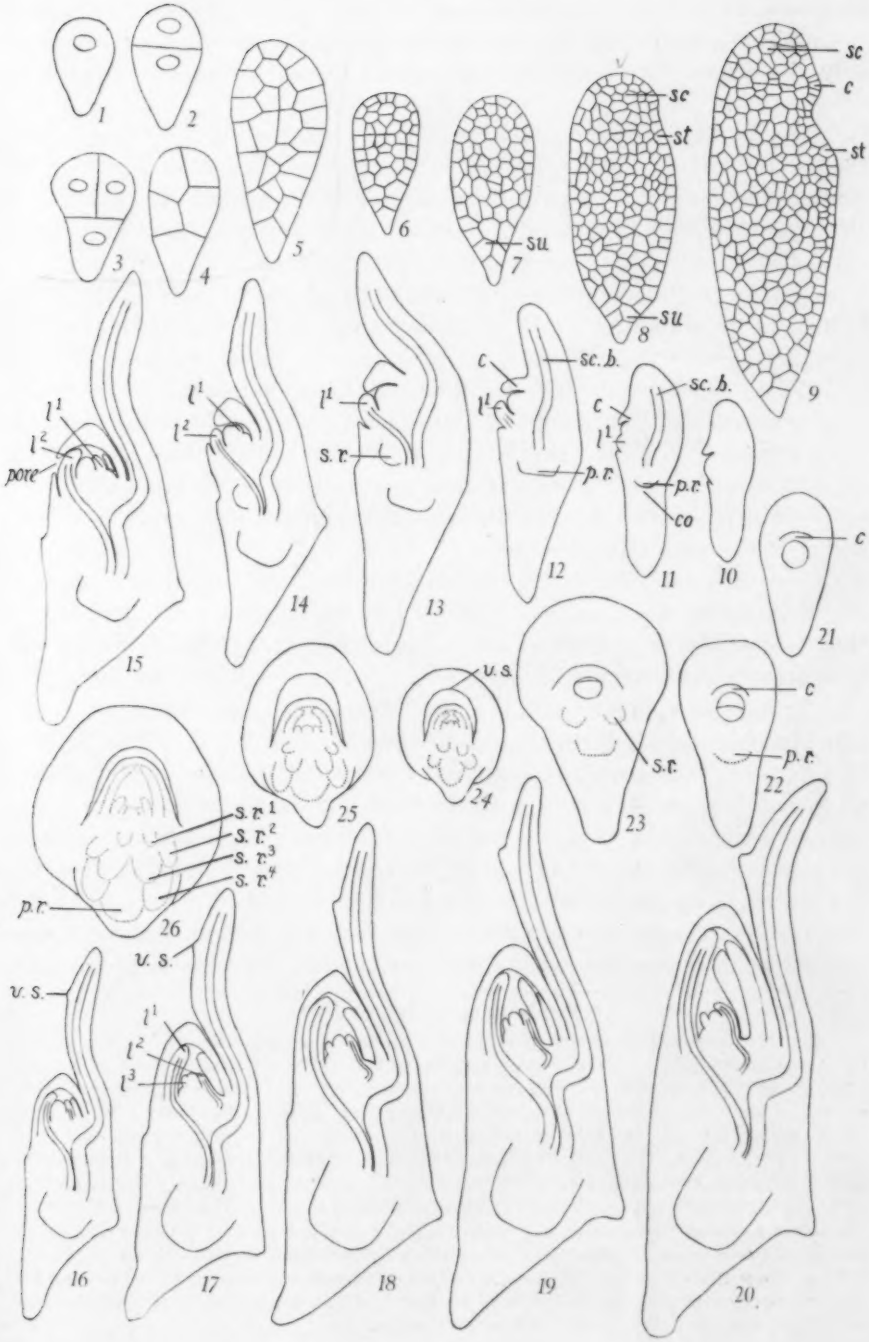
*Proembryo.* Within the first two days after fertilization the first two divisions of the zygote occurred (figs. 1, 2, 3). The first was at right angles to the long axis of the ovule and the second occurred in the apical cell and was at right angles to the plane of the first division. After this three-celled stage the divisions seemed not to take place in any definite sequence or arrangement. By the third day the proembryo was made up of from 10 to 15 cells (fig. 4) and by the fourth of about 50 (fig. 5). The rate of division remained constant for several days, as determined by counting the number of cells in embryos of different ages. During the first seven days (figs. 1–8) no differentiation was observed except that the size of cells at the tip diminished and the cells divided more rapidly than those at the base. At the same time the proembryo became club shaped and tapered to a point at the base. About eight days after fertilization (fig. 9) the upper part of the embryo began to differentiate in outline so that the part which was to become the scutellum (fig. 9 *sc.*) was distinguishable. A swelling on the face of the embryo indicated the initiation of the stem meristem (fig. 9 *st.*), and above it the coleoptile began as a slight ridge (fig. 9 *c.*).

*Scutellum.* The portion of the eight-day-old embryo (fig. 9 *sc.*) which developed into the scutellum was 0.12 mm. long, 0.12 mm. wide, and 0.08 mm. thick; the measurement of the length being arbitrarily made on the basis of comparison with older embryos. The scutellum of the fully developed embryo (fig. 28 *sc.*) was 2.6 mm. long, 2.2 mm. wide, and 0.25 mm. thick. Consequently the developing scutellum grew somewhat more in length than in width, and the growth in thickness was slight in comparison to that in the other two dimensions. The fully developed scutellum was less than twice as many cells thick as the region from which it developed (figs. 36 and 42).

No definite meristem was observed in the scutellum, but most of the divisions seemed to occur in the layers towards the surface. The lower limit of the scutellum became clearly defined after about 13 days by an angle formed between the back of the scutellum and the lower side of the coleorhiza, which

**Explanation of figures 1–26**

FIGS. 1–19. Longitudinal sections of embryos at daily stages from a fertilized egg to an embryo eighteen days old. 1–5 ×375. 6–9 ×165. 10–13 ×54. 14–15 ×40. 16–19 ×30. FIG. 20. Longitudinal section of an embryo twenty-one days old. ×30. FIGS. 21–26. Face views of whole embryos cleared in xylene; nine, ten, twelve, fifteen, seventeen, and twenty-eight days old respectively. 21–23 ×54. 24–26 ×17. *c*, coleoptile; *co*, coleorhiza; $l^1$, first leaf; $l^2$, second leaf; $l^3$, third leaf; *sc.* scutellum; *sc.b.*, scutellar bundle; *s.r.*, seminal root; *st*, stem meristem; *su*, suspensor; *v.s.*, ventral scale.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became more acute as the development proceeded (figs. 12–14). The apex of the angle was coincident with the end of the endosperm which was undoubtedly the cause of this distinct boundary between the scutellum and the coleorhiza.

After 14 days periclinal divisions began to take place in certain cells in the ventral surface of the scutellum so that a ridge (figs. 16 and 24 *v.s.*) was produced which formed an arc from one side of the base of the coleoptile to the other side. This ridge finally extended about five cells above the surface and has been called the ventral scale by other authors.

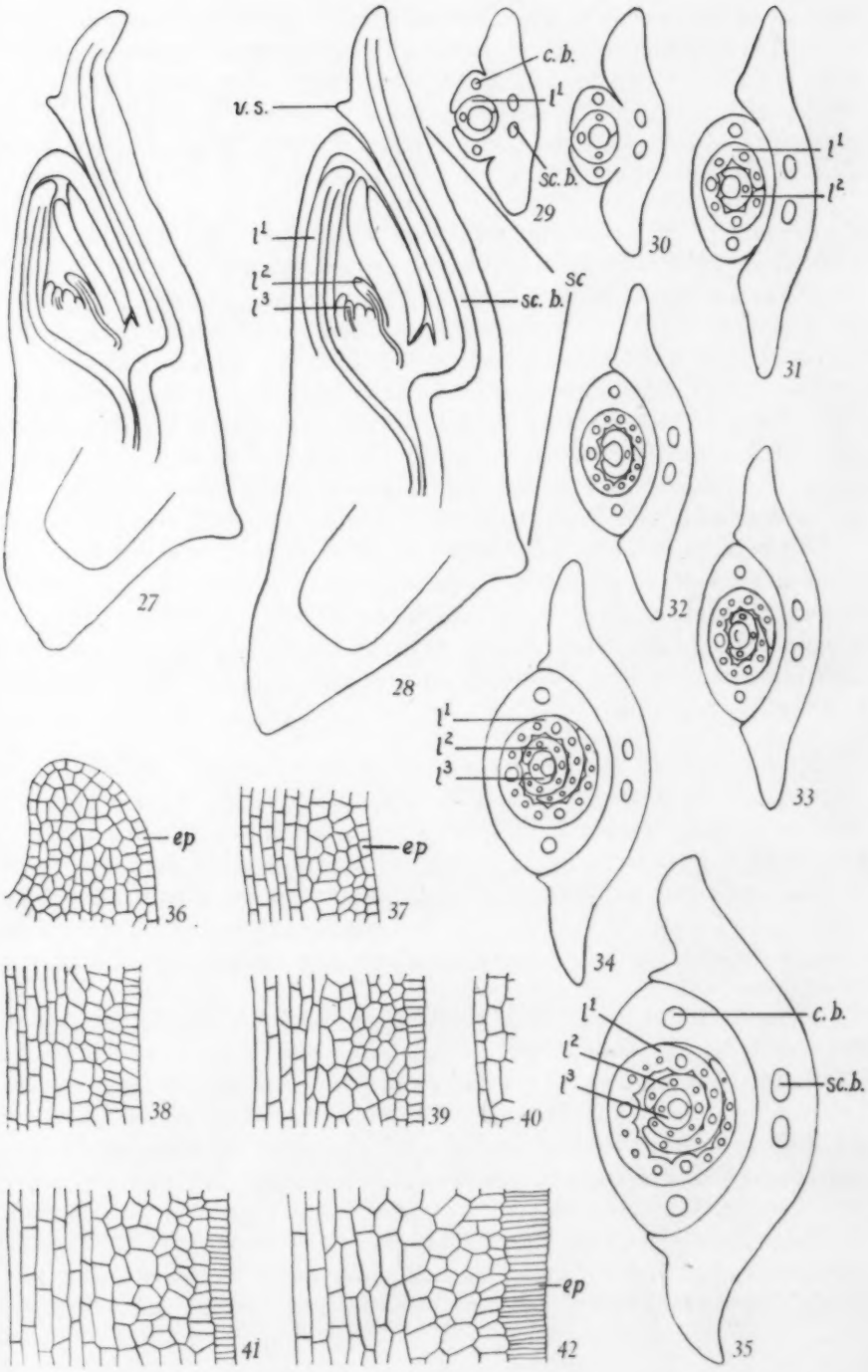
From 10 to 12 days after fertilization the epidermal cells on the dorsal surface of the scutellum, which is the surface in contact with the endosperm, appeared smaller than the internal cells or other epidermal cells (figs. 36 and 37 *ep.*). On about the 16th day these cells began to elongate in the dimension perpendicular to the surface and became recognizable as the epithelial layer (figs. 38, 39, 41 *ep.*). In the fully developed embryo these cells (fig. 42 *ep.*), in which the cytoplasm was more opaque than in the other cells, were three times as long as those of the same tissue on the 10th day (fig. 36 *ep.*) and were less than a third as wide.

The epidermal cells on the ventral surface of the scutellum within the ventral scale increased in length parallel to the long axis of the embryo so that they were several times as long as wide (figs. 41, 42). Similar epidermal cells outside the ventral scale were only slightly elongated (fig. 40).

The bundles of the scutellum were differentiated, ten days after fertilization, as two strands of elongated cells (figs. 11, 29, *sc.b.*). The lines in figure 11 are merely a diagrammatic outline of one bundle. These bundles formed an S-shaped curve on a level with the base of the stem meristem in the 11-day-old embryo (fig. 12 *sc.b.*) and the inflections became more pronounced as the embryo developed (figs. 12–20, 28 *sc.b.*). The bundles elongated with the growth in length of the scutellum and branched toward the outer edges. The branches turned back toward the base of the scutellum. The bundles increased in thickness throughout the development (figs. 29–35 *sc.b.*) by an

**Explanation of figures 27–42**

FIG. 27. Longitudinal section of an embryo twenty-eight days old. × 30. FIG. 28. Longitudinal section of the embryo of a mature grain soaked for twenty-four hours. × 30. FIGS. 29–34. Cross sections through the stem meristem of embryos twelve, thirteen, fifteen, sixteen, seventeen, and twenty-one days old respectively. 29–31 × 40. 32–34 × 30. FIG. 35. Cross section through the stem meristem of the embryo of a mature grain soaked for twenty-four hours. × 30. FIGS. 36–39, 41. Median longitudinal sections of a corresponding portion of the scutellum within the ventral scale of embryos ten, twelve, fifteen, eighteen, and twenty-one days old respectively. × 165. FIG. 40. Longitudinal section of the ventral surface of the scutellum outside the ventral scale of the embryo of a mature grain soaked for twenty-four hours. × 165. FIG. 42. Median longitudinal section within the ventral scale of the scutellum of the embryo of a mature grain soaked for twenty-four hours. × 165. *c.b.*, coleoptilar bundle; *ep*, epithelium; $l^1$, first leaf; $l^2$, second leaf; $l^3$, third leaf; *sc*, scutellum; *sc.b.*, scutellar bundle; *v.s.*, ventral scale.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increase in the number of cells. The phloem and xylem could not be distinguished in the bundles of the normal embryos, but from the cultured plants it was found that even in the bundles of 10-day-old embryos some of the cells were potentially xylem and some phloem. Also from these plants it was determined that the bundles were collateral, with the xylem on the ventral side, as has been reported for other grass embryos.

*Coleoptile.* The coleoptile was formed from the general region of the proembryo which also gives rise to the scutellum (fig. 9 *c.*) and first appeared as a crescent-shaped ridge above the stem meristem (fig. 21 *c.*). This ridge was extended downward until it encircled the growing point and then grew out from the rest of the embryo as a sheathing tube. The sides of the tube gradually approach each other so as to leave a narrow vertical slit or pore, through which the shoot emerges during germination. The side next to the scutellum grew faster than the other side so that the pore became located on the front side of the coleoptile (fig. 15 pore). In the later stages the ratio of the number of cells above and below the pore remained about the same.

The bundles began to differentiate on about the 11th day opposite each other on the sides of the coleoptile (fig. 29 *c.b.*). The size of the bundles increased throughout the development of the embryo by an increase in the number of cells (figs. 29–35 *c.b.*). From the cultured plants it was determined that these bundles were collateral with the xylem on the side toward the center of the coleoptile.

*Stem Meristem.* By going back through the stages of the developing embryo the region which was to become the stem meristem was recognized seven or eight days after fertilization (figs. 8, 9 *st.*). It began as a swelling on the face of the embryo due to the higher frequency of cell divisions in that part. The cells were smaller than those of the surrounding part of the embryo (fig. 9 *st.*). The size of the meristem was constant throughout the development of the embryo, though there was some variation at different points in each plastochron.

On the 10th day the first leaf primordium was initiated (fig. 11 $l^1$), and the midvein of the first leaf began to differentiate on about the 12th day (fig. 29 $l^1$). In the embryo of the mature grain there were nine pairs of lateral bundles in the first leaf (fig. 35 $l^1$). Counting from the midvein, pair four was differentiated on the 13th day (fig. 30), pairs two and seven on the 15th day (fig. 31 $l^1$), pairs three and five on the 16th day (fig. 32), pair one on the 17th day (fig. 33), and pairs six, eight, and nine on the 21st day (fig. 34 $l^1$).

The primordium of the second leaf was first observed in the 13-day-old embryo (fig. 14 $l^2$). Its midvein began to differentiate on the 15th day (fig. 31 $l^2$). There were three pairs of lateral bundles in the second leaf of the fully

developed embyro (fig. 35 $l^2$). Pair 2 began to differentiate in the 17-day-old embryo (fig. 33), and pairs 1 and 3 in the 21-day-old embryo (fig. 34 $l^2$).

The primordium of the third leaf appeared on about the 16th day (fig. 17 $l^3$). The midvein of this leaf differentiated on the 21st day (fig. 34 $l^3$), and no other bundles were formed in the third leaf in the normal development of the embryo (fig. 35 $l^3$).

*Root System.* The primary root primordium began to develop about 10 days after fertilization (figs. 11, 22 *p.r.*). In the cultured plants the primary root had eight strands of protoxylem alternating with eight strands of phloem as did the other roots formed in the embryo. The number of cells in each strand increased with the age of the embryo, and the cortex of the roots also increased in thickness. The first pair of seminal roots began to differentiate on the 12th day (figs. 13, 23 *s.r.*). The second pair began on the 15th day above and between the first pair (fig. 24). The third pair was formed outside and above the second pair on the 17th or 18th day (fig. 25). A fourth pair of primordia was formed after 21 days between and slightly above the third pair (fig. 26 *s.r.*). All of these primordia were formed in front of the primary root.

*Coleorhiza.* The coleorhiza was differentiated from the lower part of the 10-day-old embryo (fig. 11 *co.*) by the development of the primary root primordium. The other root primordia grew down within the coleorhiza and were often separated from each other by thin layers of the tissue of the coleorhiza. The coleorhiza grew partly by cell elongation but mostly by scattered cell divisions. No vascular bundles were formed in this part of the embryo.

*Suspensor.* The cells near the base of the proembryo were larger than those in the other parts (figs. 7 and 8 *su.*) and stopped dividing after about 10 days. They formed the suspensor, which was not more than 0.1 mm. long and which in the fully developed embryo was no longer recognizable.

*Transition Region of the Primary Root.* The metaxylem of the primary root was connected to the midvein and the second, fourth, and seventh pairs of lateral bundles of the first leaf. The protoxylem and a little of the metaxylem were connected to the scutellar bundles.

Part of the phloem strands of the primary root passed into the center of the transition region and formed a large mass of phloem. This mass was observed to divide into two parts higher up in the region. One portion was traced to the midvein of the first leaf and the rest to the phloem of the fourth and seventh lateral bundles of the first leaf and to the scutellar bundles. The remainder of the phloem of the primary root was connected to the second pair of lateral bundles and to the scutellar bundles.

*Vascular Relationships.* The two bundles of the scutellum were connected with the primary root as it began to develop on the 10th day. The two bundles of the coleoptile began to differentiate on the 12th day and soon became connected with the bundles of the scutellum. At the base of the coleoptile the bundles from it turned at right angles and passed back around the other bundles, and joined the scutellar bundles where the latter made the second bend to pass down to the transition region.

The midvein of the first leaf passed alone through the transition region to the primary root, though the second pair of lateral bundles of the first leaf came very close to it as they were differentiated in the same region. The fourth and seventh pairs of lateral bundles of the first leaf were so close together in the transition region that they practically constituted a single pair of bundles. The connections of the other bundles of the stem were not differentiated in the normal embryos, but in the cultured plants the bundles turned at right angles above the transition region of the primary root and entered the transition regions of the other seminal roots. These latter regions were so close together that they formed a very complicated plate in the front of the embryo.

## DISCUSSION

Since the cell walls formed by the first two divisions of the zygote were observed to be at right angles to each other, whereas Norner (1881) and Souèges (1924) found them to be parallel, and since the subsequent divisions are even more irregular, it would seem that no special significance can be attached to the sequence of cell divisions nor to the arrangement of the cells in the development of the embryo. This is in agreement with the findings of Randolph (1936) and may be interpreted as an indication that the factors controlling the growth of the embryo affect the embryo as a whole rather than definite individual cells. Souèges' (1924) stated that the parts of the embryo are already determined in particular cells in the 16-celled embryo.

The smaller size and greater number of cells in the upper part of the proembryo after about four days suggest a gradient from the apex to the base of some factors which control the rate of division of the cells. The appearance of smaller cells and more division figures in certain parts of the embryo on about the seventh day seems to indicate that similar factors had become concentrated in those regions.

In the developing scutellum the cells are larger than elsewhere and the divisions are scattered, so that there seems to be no localization of such factors in that part.

In the development of the embryo the region which is to become the scutellum can be distinguished from that part which becomes the stem meristem. The coleoptile develops from the same region as that which gives

rise to the scutellum. Because of this the scutellum and the coleoptile are considered to be closely associated parts distinct from the stem. There are other indications of this distinction which, while they cannot be offered as proof, add to the support of the conclusion based on the development of the embryo. These are as follows.

The bundles of the scutellum develop before the bundles of the stem and are connected directly with the primary root. However this does not prove that the scutellum is morphologically distinct from the stem, since the midvein of the first leaf also is connected directly with the primary root and has no connections with any of the other bundles of the stem.

The connection of the coleoptilar bundles with the scutellar bundles indicates a closer relationship between the coleoptile and the scutellum than between either of them and the stem. In *Hordeum* the coleoptile and scutellum are similar in possessing two bundles in contrast to the one main bundle of the foliage leaves. The scutella of some of the wild species of *Hordeum* and of other grasses have only one bundle, and whether one bundle or two is the primitive condition is difficult to determine. In the corresponding structure of the embryos of other monocotyledons, which are usually considered to be less specialized than grass embryos, there are usually two and sometimes four bundles (Taylor 1921).

The scutellum and coleoptile are different in appearance and function from the foliage leaves, but this point should not be stressed, since foliage leaves are known to be greatly modified. While these additional indications of the separation in question cannot be defended as proof, it is equally difficult to find any conclusive evidence that the two structures are modified foliage leaves. It seems possible to consider them merely structures peculiar to the embryo.

The scutellum alone or the scutellum and the coleoptile together have been generally considered as the cotyledon of the embryo. The term cotyledon, according to the Oxford English Dictionary, "was first used in the botanical sense by Linnaeus as referring to those seed leaves which are not in themselves depositories of nutriment but act as organs of absorption, in which he saw an analogy to the function of the cotyledon in the zoological sense." The term had been previously applied to the lobes on certain mammalian placentae. If such a meaning is to be preserved, then the scutellum of grass embryos is more rightfully called a cotyledon than any other structure of the embryo of any other plant, since with the development of the epithelial layer it is certainly the structure most specialized for absorption. From the standpoint of development it is concluded that the scutellum is homologous with the cotyledon of other monocotyledonous embryos.

The various views of the homologies of the parts of the grass embryo have caused much confusion on the terminology of that part of the axis between

the node of the first foliage leaf and the primary root. In *Hordeum* as in other grasses this region is very complex. The lower portion is covered by the coleorhiza on the outer face and by the scutellum on the inner face. Just above the primary root is the transition region from it to seven of the bundles of the first leaf and to the scutellar bundles. Above this are the four pairs of seminal roots and the transition regions through which the bundles of the stem are connected with them. The coleoptilar bundles are present in this region from the divergence of the coleoptile to the point where they connect with the scutellar bundles.

Van Tieghem (1872), Avery (1930), Boyd and Avery (1936), and others have shown that this region varies in different species of grasses; it does not, therefore, seem possible to find a natural term which will fit them all. Van Tieghem (1872) divided the grass embryos he studied into three groups on the basis of the morphology of the region. In the members of the first group the coleoptile is inserted just above the scutellum, as in *Hordeum* and *Triticum*. In those of the second group the coleoptile is inserted some distance above the scutellum and the region is traversed by a "cortical" bundle, as in *Avena* and *Zizania*. In plants of the third group the coleoptile is inserted some distance above the scutellum and the region between is not traversed by a cortical bundle, as in the embryo of *Zea*.

Avery (1930) described the anatomy of the seedlings of *Triticum*, *Avena*, and *Zea*, showing the differences between the three groups of Van Tieghem's classification. The cortical bundle of the second, or *Avena*, type is the scutellar bundle which extends almost to the divergence of the coleoptile where the coleoptilar bundles connect with it. From this point according to Avery (1930) a "common bundle" passes down to the primary root. Avery (1930) and Boyd and Avery (1936) regarded the scutellar bundle as extending only to the point where it met the coleoptilar bundles. However, in the ten-day embryo of *Hordeum* two bundles connect the scutellum with the primary root meristem and no coleoptilar bundles are present. In this case it is not possible to distinguish the "scutellar trace" from the "common bundle" as described by Boyd and Avery (1936). From the development of the embryo in *Zizania*, an embryo of the *Avena* type, as illustrated by LaRue and Avery (1938) it also appears that the "common bundle" cannot be distinguished from the "scutellar trace" at an early age. In the *Zea* embryo as described by Avery (1930) the scutellar bundle does not extend up into the region between the scutellum and the coleoptile. According to Avery (1930) the coleoptilar bundles diverge from two bundles in the stele. It seems more consistent with the condition in other embryos to consider that the coleoptilar bundles extend down through the region in question and connect with the scutellar bundles. In the *Hordeum* embryo there is no elongation of the axis between the scutellum and the divergence of the coleoptile, and the coleoptilar bundles are clearly connected with the scutellar bundles.

It is suggested that in the second, or *Avena*, type of embryo the "meristematic region" described by Avery (1930) is in a part of the scutellum, and that the region of the axis between the level of divergence of the scutellum and the coleoptile is the transition region between the stem and the primary root surrounded by an elongated portion of the scutellum. In the third, or *Zea*, type the absence of a cortical bundle in the region between the scutellum and the divergence of the coleoptile is due to the fact that the "meristematic region" as shown by Avery (1930) is above the scutellar bundle. The bundles from the coleoptile extend through this region to connect with the scutellar bundle, and so it is considered that in this type of embryo the region between the divergence of the scutellum and that of the coleoptile is part of the transition region between the primary root and the stem, surrounded by and fused with an elongated portion of the coleoptile.

As has been pointed out, it does not seem possible to find one natural term which will accurately describe the condition in all the types of grass embryos. It is the writer's belief that the terms which have been applied to this region are not strictly correct, but developing a new artificial term would only add to the confusion.

This investigation was begun while the author was an assistant in the Department of Botany, University of Michigan, and was completed while he held the Emma Cole Fellowship in Botany from the same institution. The writer wishes to express his appreciation of the support which has made this work possible. It is a pleasure to acknowledge the suggestions and criticisms of Professor C. D. LaRue, of the University of Michigan, under whose guidance this work was done, and the generous assistance of Professor David R. Goddard, of the University of Rochester, in the preparation of the manuscript.

## SUMMARY

1. The normal development of the embryo of *Hordeum sativum* is described, and the development of the vascular system of the embryo is interpreted from plants grown in culture from embryos of different ages.

2. The proembryo develops with no definite arrangement or sequence of cell divisions.

3. The scutellum and stem meristem begin to differentiate at eight days after fertilization.

4. The coleoptile is formed from the region which becomes the scutellum and is closely associated with the scutellum.

5. The scutellum and the coleoptile are considered to be structures morphologically distinct from the foliage leaves and peculiar to the embryo.

6. The time of differentiation of the leaf primordia, the bundles of the leaves, and the seminal root primordia is given.

7. The vascular relationships of the various parts of the embryo are described.

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## Literature Cited

**Avery, G. S., Jr.** 1930. Comparative anatomy and morphology of embryos and seedlings of maize, oats, and wheat. Bot. Gaz. **89:** 1–39.

**Boyd, Lucy & Avery, G. S., Jr.** 1936. Grass seedling anatomy: The first internode of *Avena* and *Triticum*. Bot. Gaz. **97:** 765–779.

**Bruns, E.** 1892. Der Grasembryo. Flora **76:** 1–35.

**Čelakovský, L. J.** 1897. Ueber die Homologien des Grasembryos. Bot. Zeit. **55:** 141–174.

**LaRue, C. D. & Avery, G. S., Jr.** 1938. The development of the embryo of *Zizania aquatica* in the seed and in artificial culture. Bull. Torrey Club **65:** 11–21.

**McCall, M. A.** 1934. Developmental anatomy and homologies in wheat. Jour. Agr. Res. **48:** 283–321.

**Norner, C.** 1881. Embryoentwickelung der Gramineen. Flora **64:** 241–251; 257–266; 273–284.

**Randolph, L. F.** 1936. Developmental morphology in the caryopsis of maize. Jour. Agr. Res. **53:** 881–916.

**Souèges, R.** 1924. Embryogénie des graminées: Développement de l'ambryon chez le *Poa annua* L. Compt. Rend. Acad. Sci. Paris **178:** 860–862.

**Taylor, W. R.** 1921. The embryogeny of *Cyrtanthus parviflorus* Baker. Am. Jour. Bot. **8:** 502–506.

**Van Tieghem, P.** 1872. Observations anatomique sur le cotylédon des gramineés. Ann. Sci. Nat. Bot. (V) **15:** 236–276.

———. 1897. Morphologie de l'embryon et de la plantule chez les graminées et les cyperacées. Ann. Sci. Nat. Bot. (VIII) **3:** 259–309.

# INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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**Abbott, E. V. & Tippett, R. L.** *Myriogenospora* on sugar cane in Louisiana. Phytopathology **31:** 564–566. *f. 1.* Je 1941.

**Allard, H. A.** Some plants found in northern Virginia and West Virginia. Va. Jour. Sci. **2:** 116–119. My 1941.

**Allard, H. A. & Evans, M. W.** Growth and flowering of some tame and wild grasses in response to different photoperiods. Jour. Agr. Res. **62:** 193–228. *illust.* 15 F 1941.

**Almeida, F. & Simões Barbosa, F. A.** Contribuição para o estudo de *Cephalosporium recifei.* Arq. Inst. Biol. Sao Paulo **11:** 1–4. *pl. 1.* 1940 [1941].

**Ames, O.** A new *Scaphyglottis* from Mexico. Am. Orchid Soc. Bull. **10:** 49. *pl. 2.* 1 Jl 1941.

**Anderson, E. G.** Translocations in maize involving the short arm of chromosome I. Genetics **26:** 452–459. 1 Jl 1941.

**Apolinar Maria, H.** Vocabulario de terminos vulgares en historia natural Colombiana. Rev. Acad. Colomb. **4:** 38–46. *illust.* S–D 1940.

**Arango, R. J.** Monografias botanicas La Granadilla. Univ. Antioquia no. 45: 75–80. Ap–My 1941.

**Archer, C. J.** The starch cycle in the Hachiya persimmon. Proc. Am. Soc. Hort. Sci. **38:** 187–190. *f. 1, 2.* Ap 1941.

**Augustine, D. W.** Plants of Mahaska County, Iowa. Proc. Iowa Acad. Sci. **47:** 135–154. My 1941.

**Babcock, E. B.** New species and changes in nomenclature in *Crepis.* Univ. Cal. Publ. Bot. **19:** 399–404. 26 Je 1941.

**Bannon, M. W.** Vascular rays and adventitious root formation in *Thuja occidentalis* L. Am. Jour. Bot. **28:** 457–463. *f. 1–27.* 8 Jl 1941.

**Barducci, T. B. & Madoo, R. M.** Investigaciones acerca del parentesco de la especie peruana de algodonero *Gossypium Raimondii* Ulbrich. Minist. Fom. Dir. Agr. Ganad. (Lima) Bol. **22:** 1–29. *illust.* Mr 1941.

**Bartlett, H. H.** The reports of the Wilkes expedition, and the work of the specialists in science. Proc. Am. Phil. Soc. **82:** 601–705. 29 Je 1940.

**Beal, J. M.** Cytological studies in relation to the classification of the genus *Calochortus.* II. Bot. Gaz. **102:** 810, 811. *f. 1–3.* 2 Jl 1941.

**Beetle, A. A.** Studies in the genus *Scirpus* L. II. The section *Bacothryon* Ehrb. Am. Jour. Bot. **28:** 468–476. 8 Jl 1941.

**Bellows, J. M. & Bamford, R.** Megagametophyte development in a triploid tulip. Bot. Gaz. **102:** 699–711. *f. 1–43.* 2 Jl 1941.

**Berger, C. A.** Reinvestigation of polysomaty in *Spinacia*. Bot. Gaz. **102**: 759–769. *f. 1–18*. 2 Jl 1941.

**Berry, E. W.** *Liriodendron* in the Miocene of America and Eastern Asia. Torreya **41**: 82–84. *1 f.* My–Je 1941.

**Biale, J. B.** Periodicity in transpiration of lemon cuttings under constant environmental conditions. Proc. Am. Soc. Hort. Sci. **38**: 70–74. *f. 1–2*. Ap 1941.

**Bitancourt, A. A. & Jenkins, A. E.** Novas especies de *Elsinoë* e *Sphaceloma* sobre hospedes de importancia economica. Arq. Inst. Biol. São Paulo **11**: 45–58. *pl. 11–25*. 1940 [1941].

**Blackmon, G. H.** Boron in pecan nutrition. Proc. Am. Soc. Hort. Sci. **38**: 209, 210. Ap 1941.

**Blackmon, G. H.** Nitrogen content of dormant pecan twigs. Proc. Am. Soc. Hort. Sci. **38**: 211, 212. Ap 1941.

**Blum, J. L.** Responses of sunflower stems to growth-promoting substances. Bot. Gaz. **102**: 737–748. *f. 1–10*. 2 Jl 1941.

**Boehner, P.** A check list of the hepatics of Cattaraugus County, N. Y.—A preliminary survey of the county. Sci. Stud. St. Bonaventure Coll. $9^2$: 14–16, 28. Ja 1941.

**Boehner, P.** A preliminary check list of mosses found in Cattaraugus County, N. Y. Part I. Musci Acrocarpi. Sci. Stud. St. Bonaventure Coll. $9^3$: 4–6. Mr 1941. Part II. Musci Pleurocarpi. $9^4$: 4–7, 28. Je 1941.

**Boehner, P.** The *Sphagna* of Cattaraugus County, N. Y. Sci. Stud. St. Bonaventure Coll. $9^2$: 3–5, 12. Ja 1941.

**Borthwick, H. A., Parker, M. W. & Heinze, P. H.** Influence of localized low temperature on Biloxi soybean during photoperiodic induction. Bot. Gaz. **102**: 792–800. *f. 1, 2*. 2 Jl 1941.

**Boynton, D., Reuther, W. & Cain, J. C.** Leaf analysis and apparent response to potassium in some prune and apple orchards. Proc. Am. Soc. Hort. Sci. **38**: 17–20. *f. 1, 2*. Ap 1941.

**Brass, L. J.** The 1938–39 expedition to the Snow Mountains, Netherlands New Guinea. Jour. Arnold Arb. **22**: 271–295. 17 Ap 1941. 297–342. *pl. 1–7*. Jl 1941.

**Braun, E. L.** The differentiation of the deciduous forest of the eastern United States. Ohio Jour. Sci. **41**: 235–241. My 1941.

**Brierley, P.** Effect of cool storage of Easter lily bulbs on subsequent forcing performance. Jour. Agr. Res. **62**: 317–335. *illust*. 15 Mr 1941.

**Brown, N. A.** Tumors on elm and maple trees. Phytopathology **31**: 541–548. *f. 1–3*. Je 1941.

**Bryant, L. R. & Beach, G. A.** A preliminary study of chlorosis in American grapes. Proc. Am. Soc. Hort. Sci. **38**: 395, 396. Ap 1941.

**Bukasov, S. M.** The geography of the endemic potatoes of South America. Rev. Arg. Agron. **8**: 83–104. Je 1941.

**Buller, A. H. R.** The diploid cell and the diploidisation process in plants and animals, with special reference to the higher fungi. I. Bot. Rev. **7**: 335–387. Jl 1941. II. 389–431. Au 1941.

**Burnham, C. R.** Cytogenetic studies of a case of pollen abortion in maize. Genetics **26**: 460–468. 1 Jl 1941.

**Butler, L.** The inheritance of fruit size in the tomato. Canad. Jour. Res. **19**: 216–224. Je 1941.

**Carabia, J. P.** Las Bromeliaceas de Cuba. II. Mem. Soc. Cub. Hist. Nat. **15**: 245–258. Jl 1941.

**Castañeda, M.** A new cactus. Cactus & Succ. Jour. **13:** 98, 99. *f. 52, 53.* Je 1941.

**Chambers, R.** Blue nuclei in tulip petals. Am. Jour. Bot. **28:** 445, 446. *f. 1.* 8 Jl 1941.

**Clark, N. A. & Frahm, E. E.** The effect of various growth-promoting substances on the reproduction of *Lemma.* Proc. Iowa Acad. Sci. **47:** 239–247. My 1941.

**Clausen, R. E.** Polyploidy in *Nicotiana* with discussion by Dr. Harold H. Smith. *In* Symposium on theoretical and practical aspects of polyploidy in crop plants. Am. Nat. **75:** 291–309. Jl–Au 1941.

**Conard, H. S.** Liverworts of the so-called unglaciated area of Iowa. Proc. Iowa Acad. Sci. **47:** 91–95. *f. 1, 2.* My 1941.

**Conard, H. S.** Thirty Iowa liverworts. Proc. Iowa Acad. Sci. **47:** 97–99. My 1941.

**Condit, I. J. & Horne, W. T.** Further notes on fig mosaic. Phytopathology **31:** 561–563. *f. 1, 2.* Je 1941.

**Constance, L.** The genus *Nemophila* Nutt. Univ. Cal. Publ. Bot. **19:** 341–398. *f. 1–13.* 3 Jl 1941.

**Copeland, E. B.** *Holttumia,* genus novum. Philippine Jour. Sci. **74:** 153. *pl. 1.* F 1941.

**Correll, D. S.** Studies in *Isochilus, Mormodes* and *Hexalectris.* I–IV. Harvard Bot. Mus. Leafl. **10:** 1–20. *f. 1, 2.* 25 Je 1941.

**Croasdale, H. T.** Additional records of marine algae from New Hampshire. Rhodora **43:** 213–216. *f. 1.* 13 Je 1941.

**Croizat, L.** The tribe Plukenetiinae of the Euphorbiaceae in eastern tropical Asia. Jour. Arnold Arb. **22:** 417–431. Jl 1941.

**Cronquist, A.** Noteworthy plants from Idaho. Madroño **6:** 87–89. 11 Jl 1941.

**Curtis, J. T.** Pelorie flowers in *Cypripedium reginae* Walt. Am. Midl. Nat. **25:** 580–583. *f. 1–4.* My 1941.

**Daniel, H.** Nuevos Alcaloides extraidos de algunas leguminosas. Univ. Antioquia no. **45:** 135–139. Ap–My 1941.

**Dermen, H.** Simple and complex periclinal tetraploidy in peaches induced by colchicine. Proc. Am. Soc. Hort. Sci. **38:** 141. Ap 1941.

**Dermen, H. & Bain, H. F.** Periclinal and total polyploidy in cranberries by colchicine. Proc. Am. Soc. Hort. Sci. **38:** 400. Ap 1941.

**Drechsler, C.** Three species of *Pythium* with proliferous sporangia. Phytopathology **31:** 478–507. *f. 1–13.* Je 1941.

**Ducke, A.** Lauráceas aromáticas da Amazonia brasileira. An. 1ª Reun. Sul-Amer. Bot. **3:** 55–65. *pl. 1–11.* 1938 [1941].

**Eckles, M. L.** Megasporogenesis and development of the megagametophyte in *Nothoscordum bivalve.* Bot. Gaz. **102:** 806–809. *f. 1–9.* 2 Jl 1941.

**Egler, F. E.** The orthography of "pensylvanicus." Rhodora **43:** 220–222. 13 Je 1941.

**El Azouni, M. M. & Cameron, S. H.** Adventitious buds in Citrus. Proc. Am. Soc. Hort. Sci. **38:** 363–368. *f. 1–5.* Ap 1941.

**Emerson, R.** An experimental study of the life cycles and taxonomy of *Allomyces.* Lloydia **4:** 77–144. *f. 1–16.* Je 1941.

**Fassett, N. C.** Preliminary reports on the flora of Wisconsin. XXIX. Anacardiaceae. Trans. Wis. Acad. Sci. **32:** 103–106. *f. 1–6.* 1940 [1941].

**Fawcett, H. S. & Bitancourt, A. A.** Occurrence, pathogenicity and temperature relations of phytophthora species on citrus in Brazil and other South American countries. Arq. Inst. Biol. São Paulo **11:** 107–118. *pl.* 32–34. 1941 [1941].

**Fernald, M. L.** The campestrian variety of *Frochlichia floridana*. Rhodora **43**: 336. Jl 1941.

**Fernald, M. L.** *Phragmites communis* versus *P. maximus*. Rhodora **43**: 286, 287. 13 Je 1941.

**Fernald, M. L.** Two forms of *Rhododendron maximum*. Rhodora **43**: 336. Jl 1941.

**Fernald, M. L.** Two varieties of *Dicliptera brachiata*. Rhodora **43**: 287, 288. 13 Je 1941.

**Fernald, M. L.** Varieties of *Acnida altissima*. Rhodora **43**: 288. 13 Je 1941.

**Filinger, G. A.** Soils and soil treatments affect the morphology of French crab roots. Proc. Am. Soc. Hort. Sci. **38**: 305–310. *f. 1–6*. Ap 1941.

**Fischer, H. E., Darrow, G. M. & Waldo, G. F.** Further chromosome studies of some varieties of blackberries. Proc. Am. Soc. Hort. Sci. **38**: 401–404. Ap 1941.

**Fosberg, F. R.** Observations on Virginia plants, Part I. Critical and distributional notes. Va. Jour. Sci. **2**: 106–111. My 1941.

**Foster, R. C.** Studies in the Iridaceae—II. Contr. Gray Herb. **136**: 3–78. 12 Jl 1941.

**Friesner, R. C.** The genus *Solidago* in West Virginia. Castanea **6**: 53–75. Ap 1941.

**[Fulling, E.]** Note on the use of the term "Plasmodesmata." Bot. Rev. **7**: 333. Je 1941.

**Gates, H. E.** A new variety. Cactus & Succ. Jour. **13**: 78. *f. 35*. My 1941.

**Gilly, C.** A note on the authorship of certain species of Cyperaceae. Rhodora **43**: 333–335. Jl 1941.

**Gilman, J. C.** Illustrations of the fleshy fungi of Iowa. I. The purple-brown-spored Agarics. Proc. Iowa Acad. Sci. **47**: 83–90. *f. 1–6*. My 1941.

**Glendening, G. E.** Development of seedlings of *Heteropogon contortus* as related to soil moisture and competition. Bot. Gaz. **102**: 684–698. *f. 1–4*. 2 Jl 1941.

**Goldberg, B.** Life history of *Peltandra virginica*. Bot. Gaz. **102**: 641–662. *f. 1–49*. 2 Jl 1941.

**González Guerrero, P.** Algas de la Republica Argentina (agua dulce). An. Jard. Bot. Madrid **1**: 141–171. *f. 1–5*. 1941.

**Goodman, G. J.** Two names in *Mentzelia*. Leafl. West. Bot. **3**: 53, 54. 17 Jl 1941.

**Grace, N. H.** Effects of phytohormone, potassium nitrate, and ethyl mercuric bromide on the germination and early growth of wheat. Canad. Jour. Res. **19**: 211–215. Je 1941.

**Greene, H. C.** Notes on Wisconsin parasitic fungi. I. Trans. Wis. Acad. Sci. **32**: 77–83. 1940 [1941].

**Greenleaf, W. H.** Sterile amphidiploids: their possible relation to the origin of *Nicotiana tabacum*. Am. Nat. **75**: 394–399. Jl–Au 1941.

**Grieco, V.** Ação do nitrito de sodio e do bisulfito de sodio sobre o crescimento do *Aspergillus niger*. Arq. Inst. Biol. Sao Paulo **11**: 147, 148. 1940 [1941].

**Grover, F.** Mary Fink Spencer. Madroño **6**: 82–84. *port. pl. 6*. 11 Jl 1941.

**Grumbles, T. L.** The comparative anatomy of the secondary xylem of four oriental species of *Celtis*. Lloydia **4**: 145–152. *f. 1–5*. Je 1941.

**Gustafson, F. G.** Probable causes for the difference in facility of producing parthenocarpic fruits in different plants. Proc. Am. Soc. Hort. Sci. **38**: 479–481. *f. 1, 2*. Ap 1941.

**Hagerup, O. & Williams, L. O.** The status of the genus *Thorvaldsenia*. Am. Orchid Soc. Bull. **10**: 23. *pl. 1*. 1 Je 1941.

**Hansen, H. P.** Paleoecology of a montane peat deposit near Lake Wenatchee, Washington. Northwest Sci. **15:** 53–65. Au 1941.

**Hansen, H. P.** A pollen study of post-pleistocene lake sediments in the upper Sonoran life zone of Washington. Am. Jour. Sci. **239:** 503–522. *f. 2, 3.* 8 Jl 1941.

**Henrici, A. T.** The yeasts, genetics, cytology, variation, classification and identification. Bacteriol. Rev. **5:** 97–179. Je 1941.

**Hirschhorn, E.** Una nueva especie de *Melanopsichium.* Notas Museo La Plata **6:** 147–151. *f. 1, 2.* 20 My 1941.

**Hitchcock, C. L.** A revision of the Drabas of western North America. Univ. Wash. Publ. Biology **11:** 1–132. *pl. 1–8.* Ap 1941.

**Hoagland, D. R.** Water culture experiments on molybdenum and copper deficiencies of fruit trees. Proc. Am. Soc. Hort. Sci. **38:** 8–12. *f. 1–3.* Ap 1941.

**Hodge, W. H.** The genus *Charianthus.* Contr. Gray Herb. **136:** 115–133. *pl. 4–6.* 12 Jl 1941.

**Hodge, W. H.** The type species of *Heliconia.* Contr. Gray Herb. **135:** 134–137. *pl. 7.* 12 Jl 1941.

**Hoehne, F. C.** 4 Orchidaceas en i leguminosa novas para a flora Brasileira. Arq. Bot. Est. S. Paulo NS **1:** 61–63. *pl. 81–85.* Ap 1941.

**Holton, C. S.** Further studies on the oat smuts, with special reference to hybridization, cytology and sexuality. Jour. Agr. Res. **62:** 229–240. *illust.* 15 F 1941.

**Hoskins, J. H. & Cross, A. T.** A consideration of the structure of *Lepidocarpon* Scott based on a new strobilus from Iowa. Am. Midl. Nat. **25:** 523–547. *f. 1–16.* My 1941.

**Howell, J. T.** Notes on *Polycarpon.* Leafl. West. Bot. **3:** 80. 17 Jl 1941.

**Howell, J. T.** Plants new to California. Leafl. West. Bot. **3:** 79, 80. 17 Jl 1941.

**Hume, E. P.** The effect of short days upon the development of fall blooming chrysanthemums. Proc. Am. Soc. Hort. Sci. **38:** 665–668. Ap 1941.

**Huskins, C. L.** Polyploidy and mutations with discussion by Dr. H. E. Warmke. *In* Symposium on theoretical and practical aspects of polyploidy in crop plants. Am. Nat. **75:** 329–346. Jl–Au 1941.

**Jameson, W.** Synopsis plantarum aequatoriensium. Anal. Univ. Ecuador **62:** 71–345. 1939 [1940]. **63:** 137–303. 1940. **74:** 279–368. 1940 [1941].

**Johnson, G. T. & Andrews, H. N.** Notes on the ecology and geographical distribution of Mississippi Myxomycetes. Am. Midl. Nat. **25:** 584–588. My 1941.

**Johnston, I. M.** El significado floristico de los arbustos communes a los desiertos norte y sudamericanos. Rev. Arg. Agron. **8:** 114–121. Je 1941.

**Jones, D. F.** Somatic segregation. Bot. Rev. **7:** 291–307. Je 1941.

**Jones, G. N.** New species of vascular plants from the north west coast. Madroño **6:** 84–86. 11 Jl 1941.

**Kempton, J. H.** Elongation of mesocotyls and internodes in Job's-tears (*Coix lachryma-jobi* L.). Jour. Wash. Acad. Sci. **31:** 261–263. *f. 1.* 15 Je 1941.

**Knott, J. E. & Claypool, L. L.** Some responses of tomato fruits to methylbromide fumigation. Proc. Am. Soc. Hort. Sci. **38:** 501–506. *f. 1, 2.* Ap 1941.

**Kramer, M. & Silberschmidt, K.** A faixa das nervuras, uma doença de virus do fumo encontrada no estado de São Paulo. Arq. Inst. Biol. São Paulo **11:** 165–188. *pl. 39–41.* 1940 [1941].

**Kramer, P. J.** Soil moisture as a limiting factor for active absorption and root pressure. Am. Jour. Bot. **28:** 446–451. *f. 1–3.* 8 Jl 1941.

**Laing, H. E.** Effect of concentration of oxygen and pressure of water upon growth of rhizomes of semi-submerged water plants. Bot. Gaz. **102:** 712–724. *f. 1–6.* 2 Jl 1941.

**Laugham, D. G.** Effect of light on growth habit of plants. Science **93:** 576, 577. 13 Je 1941.

**León, Hermano.** *Cnidoscolus* y *Victorinia* gen. nov. en Cuba y Española. Mem. Soc. Cub. Hist. Nat. **15:** 236–243. *pl. 23, 24.* 23 Jl 1941.

**Le Rosen, A. L., Went, F. W. & Zechmeister, L.** Relation between genes and carotenoids of the tomato. Proc. Nat. Acad. Sci. **27:** 236–242. My 1941.

**Leyendecker, P. J.** A taxonomic study of the genus *Galium* in Iowa. Proc. Iowa Acad. Sci. **47:** 101–113. *f. 1–10.* My 1941.

**Lillebrand, O. & Brown, J. G.** The potassium nutrition of fruit trees. III. A survey of the K content of peach leaves from one hundred thirty-five orchards in California. Proc. Am. Soc. Hort. Sci. **38:** 37–48. Ap 1941.

**Lindstrom, E. W.** Genetic stability of haploid, diploid, and tetraploid genotypes in the tomato. Genetics **26:** 387–397. 1 Jl 1941.

**Little, E. L.** Alpine flora of San Francisco Mountain, Arizona. Madroño **6:** 65–81. *pl. 5, f. 1.* 11 Jl 1941.

**Marsh, F. L.** Water content and osmotic pressure of sun and shade leaves of certain woody prairie plants. Bot. Gaz. **102:** 812–814. 2 Jl 1941.

**Martin, G. W.** On *Argynna polyhedron* (Schw.) Morgan. Jour. Wash. Acad. Sci. **31:** 309–311. *f. 1.* 15 Je 1941.

**Mason, H. L.** Alaska cedar in California. Madroño **6:** 90. *pl. 7.* 11 Jl 1941.

**Mehlquist, G. A. L.** Inheritance in the carnation, *Dianthus caryophyllus.* II. Inheritance of nine abnormal types. Proc. Am. Soc. Hort. Sci. **38:** 699–704. *f. 1.* Ap 1941.

**Meredith, C. H.** The effect of sodium nitrate on *Fusarium oxysporum cubense.* Phytopathology **31:** 564. Je 1941.

**Merrill, E. D.** A note on the dates of issue of the fascicles comprising Cosson's "Illustrationes Florae Atlanticae," 1882–1897. Jour. Arnold Arb. **22:** 455, 456. Jl 1941.

**Metcalf, F. P.** Eight new species of Leguminosae from southeastern China. Lingnan Sci. Jour. **19:** 549–563. *f. 1–8.* 26 O 1940.

**Metcalf, F. P.** Note on *Pahudia* Miquel. Lingnan Sci. Jour. **19:** 257, 258. 3 My 1940.

**Mitchell, J. W. & Whitehead, M. R.** Responses of vegetative parts of plants following application of extract of pollen from *Zea mays.* Bot. Gaz. **102:** 770–779. *f. 1–12.* 2 Jl 1941.

**Moore, E. B. & Sanford, R.** Spring flora on Farmer's Island, Lake Mills, Wisconsin. Trans. Wis. Acad. Sci. **32:** 67–76. 1940 [1941].

**Morton, C. V.** On the name of the oak fern. Rhodora **43:** 216–219. 13 Je 1941.

**Mousley, H.** A distinctive new variety of *Orchis rotundifolia* from Canada: *Orchis rotundifolia* Banks n. var. *lineata.* Canad. Field Nat. **55:** 64, 65. *1 pl.* My 1941.

**Munz, P. A.** Interesting western plants—V. Leafl. West. Bot. **3:** 49–53. 17 Jl 1941.

**Murneek, A. E.** Relative carbohydrate and nitrogen concentration in new tissues produced on ringed branches. Proc. Am. Soc. Hort. Sci. **38:** 133–136. *f. 1–3.* Ap 1941.

**Murneek, A. E.** Vitamin $B_1$ vs. organic matter for plant growth. Proc. Am. Soc. Hort. Sci. **38:** 715–717. Ap 1941.

**Newcomer, E. H.** Chromosome numbers of some species and varieties of *Vaccinium* and related genera. Proc. Am. Soc. Hort. Sci. **38**: 468–470. Ap 1941.

**Newcomer, E. H.** A colchicine-induced homozygous tomato obtained through doubling clonal haploids. Proc. Am. Soc. Hort. Sci. **38**: 610–612. *f. 1.* Ap 1941.

**Nielsen, E. L.** Grass studies, IV. Additional species new to Arkansas. Rhodora **43**: 219, 220. 13 Je 1941.

**Nielsen, E. L. & Moyle, J. B.** Forest invasion and succession on the basins of two catastrophically drained lakes in northern Minnesota. Am. Midl. Nat. **25**: 564–579. *f. 1–17.* My 1941.

**Odland, M. L. & Porter, A. M.** A study of natural crossing in peppers (*Capsicum frutescens*). Proc. Am. Soc. Hort. Sci. **38**: 585–588. Ap 1941.

**Offermann, A. M. & Vitoria, E. R.** Estudio sobre un virus productor del Marchitamiento apical de la papa. Rev. Arg. Agron. **8**: 105–113. *pl. 5.* Je 1941.

**O'Harra, R.** *Aphanorhegma patens* in Iowa. Proc. Iowa Acad. Sci. **47**: 115–122. *f. 1–22.* My 1941.

**Oosting, H. J.** Plants occurring on calcareous rock outcrops in North Carolina. Torreya **41**: 76–81. My–Je 1941.

**Parker, E. R., Turrell, F. M. & Bonner, J.** Effects of organic matter and certain growth substances on the development of young orange trees in the orchard. Proc. Am. Soc. Hort. Sci. **38**: 49–58. *f. 1.* Ap 1941.

**Peery, G. G.** Recent fossil discoveries in Burkes Garden, Virginia. Va. Jour. Sci. **2**: 120, 121. My 1941.

**Pickett, T. A. & Cowart, F. F.** Carbohydrate changes in muscadine grape shoots during the growing season. Proc. Am. Soc. Hort. Sci. **38**: 393, 394. *f. 1.* Ap 1941.

**Pickett, W. F. & Birkeland, C. J.** Common spray materials alter the internal structure of apple leaves. Proc. Am. Soc. Hort. Sci. **38**: 158–162. *f. 1–3.* Ap 1941.

**Pohl, R. W.** Preliminary reports on the flora of Wisconsin. XXX. Rhamnales. Trans. Wisc. Acad. Sci. **32**: 107–111. 1940 [1941].

**Porsild, A. E.** A relic flora on sand dunes from the Champlain Sea in the Ottawa Valley. Canad. Field Nat. **55**: 66–72. My 1941.

**Post, K.** The effect of light intensity on response of *Euphorbia pulcherrima* and *Euphorbia fulgens* to photoperiod and temperature. Proc. Am. Soc. Hort. Sci. **38**: 663–664. Ap 1941.

**Pratt, R.** Studies on *Chlorella vulgaris*. IV. Influence of the molecular proportions of $KNO_3$, $KH_2PO_4$, and $MgSO_4$ in the nutrient solution on the growth of *Chlorella*. Am. Jour. Bot. **28**: 492–497. *f. 1–7.* 8 Jl 1941.

**Quibell, C. H.** Floral anatomy and morphology of *Anemopsis californica*. Bot. Gaz. **102**: 749–758. *f. 1–38.* 2 Jl 1941.

**Ratsek, J. C., Flory, W. S. & Yarnell, S. H.** Crossing relations of some diploid and polyploid species of roses. Proc. Am. Soc. Hort. Sci. **38**: 637–654. Ap 1941.

**Rawitscher, F.** Caso de un perichaetium interessante num musgo do gênero *Leucobryum*. Arq. Inst. Biol. São Paulo **11**: 427–431. *f. 1–8.* 1940 [1941].

**Reed, F. D.** Coal flora studies: Lepidodendrales. Bot. Gaz. **102**: 663–683. *f. 1–35.* 2 Jl 1941.

**Reed, G. M.** Inheritance of smut resistance in some oat hybrids. Am. Jour. Bot. **28**: 451–457. 8 Jl 1941.

**Reed, H. S. & Beck, J. V.** The effect of zinc on the growth process. Growth **3**: 1–7. *f. 1–3.* 1939.

**Riley, G. A.** Plankton studies. IV. Georges Bank. Bull. Bingham Oceanog. Coll. **7**[4]: 1–73. *f. 1–4.* Je 1941.

**Sax, K.** The behavior of x-ray induced chromosomal aberrations in *Allium* root tip cells. Genetics **26:** 418–425. 1 Jl 1941.

**Schopf, J. M.** Notes on the Lepidocarpaceae. Am. Midl. Nat. **25:** 548–563. My 1941.

**Schubert, B. G.** *Desmodium:* Preliminary studies—II. Contr. Gray Herb. **136:** 78–115. *pl. 1–3.* 12 Jl 1941.

**Scott, D. H. & Waugh, J. G.** Treatment of peach seed as affecting germination and growth of seedlings in the greenhouse. Proc. Am. Soc. Hort. Sci. **38:** 291–298. *f. 1–3.* Ap 1941.

**Scott, L. E.** An instance of boron deficiency in the grape under field conditions. Proc. Am. Soc. Hort. Sci. **38:** 375–378. Ap 1941.

**Sears, P. B.** Postglacial vegetation in the Erie-Ohio area. Ohio Jour. Sci. **41:** 225–234. *f. 1–10.* My 1941.

**Shinners, L. H.** *Epilobium paniculatum* var. *subulatum* in Wisconsin. Rhodora **43:** 335. Jl 1941.

**Simmonds, P. M.** Rootrots of cereals. Bot. Rev. **7:** 308–332. Je 1941.

**Smith, A. C.** Studies of Papuasian plants, III. Guttiferae. Jour. Arnold Arb. **22:** 343–374. Jl 1941.

**Smith, A. C. & Bailey, I. W.** *Brassiantha*, a new genus of Hippocrateaceae from New Guinea. Jour. Arnold Arb. **22:** 389–394. *1 pl.* Jl 1941.

**Smith, E. C. & Nichols, C.** Species hybrids in forest trees. Jour. Arnold Arb. **22:** 443–454. Jl 1941.

**Smith, H. V.** A Miocene flora from Thorn Creek, Idaho. Am. Midl. Nat. **25:** 473–522. *pl. 1–14.* My 1941.

**Smith, L. B.** Bromeliaceas novas ou interessantes do Brasil. Arq. Bot. Est. S. Paulo NS **1:** 53–60. *pl. 64–80.* Ap 1941.

**Snell, W. H. & Waterman, A. M.** James Franklin Collins. Phytopathology **31:** 475–477. *port.* Je 1941.

**Sorokin, H.** The distinction between mitochondria and plastids in living epidermal cells. Am. Jour. Bot. **28:** 476–485. *f. 1–26.* 8 Jl 1941.

**Stewart, W. S.** Effectiveness of tryptophane mixtures as growth regulators. Bot. Gaz. **102:** 801–805. *f. 1, 2.* 2 Jl 1941.

**Steyermark, J. A.** A study of *Arenaria patula.* Rhodora **43:** 325–333. Jl 1941.

**Stuckey, I. H.** Seasonal growth of grass roots. Am. Jour. Bot. **28:** 486–491. 8 Jl 1941.

**Sullivan, J. T. & Chilton, S. J. P.** The effect of leaf rust on the carotene content of white clover. Phytopathology **31:** 554–557. Je 1941.

**Thériot, I.** Complement au catalogue des mousses de Cuba. IV. Mem. Soc. Cub. Hist. Nat. **15:** 211–234. *pl. 21, 22.* Je 1941.

**Thomas, W. D.** The mycorhizal fungi and mycorhizae of four coniferous plantations in the Rhine valley. Phytopathology **31:** 567–569. Je 1941.

**Thomson, J. W.** Preliminary reports on the flora of Wisconsin. XXVII. Lentibulariaceae. Trans. Wis. Acad. Sci. **32:** 85–89. *f. 1–12.* 1940 [1941].

**Thornton, B. J. & Durrell, L. W.** Weeds of Colorado. Colo. Exp. Sta. Bull. **466:** 1–125. *illust.* Ap 1941.

**Toledo, J. F.** Notas sôbre monotipico *Heterocoma* DC. Compositae-Vernonieae. Arq. Bot. Est. S. Paulo NS **1:** 71–73. *pl. 87.* Ap 1941.

**Toledo, J. F.** Sôbre a presença, no Brasil, do gênero *Sesea* Ruiz et Pavon. Arq. Bot. Est. S. Paulo NS **1:** 64–70. *pl. 86.* Ap 1941.

**Tukey, H. B. & Brase, K. D.** Failure of seedlings of apple, peach, pear and rose to respond favorably to vitamin $B_1$. Proc. Am. Soc. Hort. Sci. **38:** 339, 340. Ap 1941.

**Ullstrup, A. J.** Two physiologic races of *Helminthosporium maydis* in the corn belt. Phytopathology **31:** 508–521. *f. 1–6.* Je 1941.

**Valencia, J. I.** Especies criticas de *Trisetum* que deben pasar al genero *Deschampsia.* Rev. Arg. Agron. **8:** 122–130. *f. 1, 2.* Je 1941.

**Valleau, W. D.** Experimental production of symptoms in so-called recovered ringspot tobacco plants and its bearing on acquired immunity. Phytopathology **31:** 522–533. *f. 1–3.* Je 1941.

**Valleau, W. D. & Diachun, S.** Virus distribution in the leaves of mosaic-susceptible tobacco plants inoculated at topping time. Jour. Agr. Res. **62:** 249–254. *f. 1, 2.* 15 F 1941.

**Valleau, W. D. & Diachun, S.** Virus distribution in mosaic-resistant tobacco and its relation to pattern development in susceptible varieties. Jour. Agr. Res. **62:** 241–247. *pl. 1, 2 + f. 1.* 15 F 1941.

**Vansell, G. H.** Nectar and pollen plants of California. Revised by G. H. Vansell and J. E. Eckert. Cal. Exp. Sta. Bull. **517:** 1–76. *f. 1–63.* Ap 1941.

**[Vecchierello], H.** A check list of the more common plants found on the campus and within a range of ten miles of Saint Bonaventure College. Sci. Stud. St. Bonaventure Coll. $8^2$: 6–7. Ja 1940. Part II. $8^3$: 6–7. Mr 1940. Part III. $9^1$: 24–25, 28. N 1940. Part IV. $9^2$: 10–12. Ja 1941. Part V. $9^3$: 10–12, 39. Mr 1941. Part VI. $9^4$: 11–15, 27. Je 1941.

**Vecchierello, H.** A check list of the Myxomycetes of Cattaraugus County, N. Y. Sci. Stud. St. Bonaventure Coll. $9^1$: 21–23, 26 Je 1941.

**Wade, D. R. & Wade, D. E.** Preliminary reports on the flora of Wisconsin. XXVIII. Caprifoliaceae. Trans. Wis. Acad. Sci. **32:** 91–101. *f. 1–18.* 1940 [1941].

**Waller, A. E.** Professor John Henry Schaffner. Ohio Jour. Sci. **41:** 253–286. *port.* My 1941.

**Wareham, R. T.** Mosses of Neotoma, Hocking County, Ohio. Bryologist **44:** 56–59. 1941.

**Watson, I. A.** Inheritance of resistance to stem rust in crosses with Kenya varieties of *Triticum vulgare* Vill. Phytopathology **31:** 558–560. Je 1941.

**Waugh, J. G. & Cullinan, F. P.** The nitrogen, phosphorus, and potassium content of peach leaves as influenced by soil treatments. Proc. Am. Soc. Hort. Sci. **38:** 13–16. Ap 1941.

**Weatherby, C. A.** Lawson's type specimens. Am. Fern Jour. **31:** 59–62. Ap–My 1941.

**Weddle, C.** Two colchicine-induced polyploids of the greenhouse chrysanthemum and their progeny. Proc. Am. Soc. Hort. Sci. **38:** 658–660. Ap 1941.

**Weeks, W. D.** Chromosome number of the beach plum (*Prunus maritima*). Proc. Am. Soc. Hort. Sci. **38:** 141. Ap 1941.

**Weiss, F.** Single-spored and monoporous vs. . . .? Phytopathology **31:** 471–472. My 1941.

**Welch, W. H.** Studies in Indiana Bryophytes III. Proc. Ind. Acad. Sci. **50:** 60–67. *f. 1–25.* My 1941.

**Wenger, R.** Some effects of supplementary illumination with Mazda lamps on the carbohydrate and the nitrogen metabolism of the aster (*Callistephus chinensis* var. Heart of France). Plant Physiol. **16:** 621–628. *f. 1, 2.* Jl 1941.

**Wheeler, L. C.** *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of southern Florida. Rhodora **43:** 97–154. *pl. 654–656.* 6 Ap 1941. 168–205. *pl. 657–664.* 9 My 1941. 223–286. *pl. 665–668.* Je 1941.

**Wherry, E. T.** *Asplenium adiantum-nigrum* in Arizona. Am. Fern Jour. **31:** 97–100. *1 f.* Jl–S 1941.

**Whitaker, T. W. & Pryor, D. E.** The inheritance of resistance to powdery mildew (*Erysiphe cichoracearum*) in lettuce. Phytopathology **31:** 534–540. *f. 1, 2.* Je 1941.

**Whitaker, T. W. & Thompson, R. C.** Cytological studies in *Lactuca.* Bull. Torrey Club **68:** 388–394. *f. 1–9.* Je 1941.

**Whitebread, C.** Beware of "Lycopodium"! Am. Fern Jour. **31:** 100–102. Jl–S 1941.

**Wilcox, L. L.** Determination of boron in plant material. Chron. Bot. **6:** 370–372. *f. 1.* 5 My 1941.

**Williams, L. O.** *Dichaea trichocarpa* and *Dichaea squarrosa.* Harvard Bot. Mus. Leafl. **10:** 39, 40. 31 Jl 1941.

**Williams, L. O.** Two new *Epidendrums* from Mexico. Am. Orchid Soc. Bull. **10:** 103–105. *pl. 4.* 1 S 1941.

**Williams, L. O.** Two new species of *Scaphyglottis* from Mexico. Am. Orchid Soc. Bull. **10:** 77, 78. *pl. 3.* 1 Au 1941.

**Wolf, F. T.** A new species of *Achlya* from Costa Rica. Mycologia **33:** 274–278. *f. 1–13.* My–Je 1941.

**Worley, C. L.** Agencies affecting production of substance B by *Rhizopus suinus.* Plant Physiol. **16:** 461–480. *f. 1, 2.* Jl 1941.

**Wort, D. J.** Phasic development of Marquis spring wheat and Fulhio winter wheat. Bot. Gaz. **102:** 725–736. *f. 1, 2.* 2 Jl 1941.

**Wright, K. E. & Crandall, D. L.** Rhode Island ferns. Torreya **41:** 73–75. My–Je 1941.

**Yarwood, C. E.** Diurnal cycle of ascus maturation of *Taphrina deformans.* Am. Jour. Bot. **28:** 355–357. *f. 1–2.* My 1941.

**Young, P. A.** New genetic characters of the tomato. Am. Nat. **75:** 280–282. My–Je 1941.

**Zeller, S. M. & Evans, A. W.** Vein clearing, a transmissible disease of *Prunus.* Phytopathology **31:** 463–467. *pl. 1.* My 1941.

**Zimmerman, P. W.** Growth regulators of plants and formative effects induced by B-naphthoxy compounds. Proc. Nat. Acad. Sci. **27:** 381–388. *f. 1–3.* Au 1941.